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On certain Points in the Morphology of the Cystidea.

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(Plate I.)

1. The Body Plates.

In many Cystideans the plates enclosing the dorsal part of the body are as regularly arranged as in the cup of a Crinoid, and various comparisons have been drawn between the two. Gottsche*, for example, has endeavoured to find a correspondence between the calyx of *Hemicosmites* and that of *Actinocrinus*, which has a hexagonal base consisting of three equal plates. The supposed base of *Hemicosmites* is also hexagonal, but is composed of four plates, two large and two small (Pl. I. fig. 1; *ib*, 1–4). Gottsche supposes that the suture between the two larger ones indicates the position of the anal interradius, and he describes the cup as consisting of "4 B, 5 R′, 3 R″ (schmal, rechteckig), 5 IR′, von denen eines direct mit der Basis articulirt, und 2 IR″ über diesem unpaaren IR′."

One great objection to this analysis is that the supposed azygos

* Sitz.-Ber. Ges. Nat. Freunde Berlin, 1886, p. 13.

IR′ obviously belongs to the second cycle of plates (Pl. I. fig. 1. 8), while the two IR″ resting upon it (15, 16) are members of the third cycle, the other four plates of which Gottsche also calls IR′ (11, 12, 14, 17). Alternating with them are the three plates which Gottsche calls second radials (A, 13, 18). It appears to me, however, that the symmetry of *Hemicosmites* is hexamerous, and not pentamerous, as Gottsche and others have supposed; and I also believe the base to be dicyclic. The four plates of the proximal series, called basals by Hall * and Gottsche, are infrabasals (Pl. I. fig. 1; *ib*, 1–4), two of them being double plates, just as in the pentamerous *Codiacrinus*, *Hypocrinus*, and *Sagenocrinus*. The tripartite monocyclic base of *Platycrinus* and the Blastoids is an analogous case. The six plates of the second cycle (5–10), Hall's subradials, which alternate in position with those of the first, are the basals (*b*). This basal ring supports a series of nine plates, six of which (*r*) alternate with the basals, and are, I believe, the radials; while the other three (A, 13, 18) which rest upon the three anterior basals are interradials (*i*). *Caryocrinus* (Pl. I. fig. 2) has only two of these (13, 18), the median anterior one being unrepresented in that type. But in other respects the lower part of its cup is entirely similar to that of *Hemicosmites*, and its hexamerous symmetry is even more strongly marked. This is well shown by the fact that each of the two large infrabasals (2, 3) is marked by two double rows of hydrospire-pores, which terminate respectively at the distal angles of the plate, just as the median row on each of the two smaller infrabasals terminates at its distal angle. There are thus six double rows of pores, and at the distal angle of every infrabasal the double row gives rise to two other rows, one upon each of the basals which rest upon it. It is true that these six basals (5–10) are not all of the same shape or size; but I do not see how any one can doubt that they are all morphologically equivalent, and belong to the same cycle of plates. Von Buch laid great stress upon this point † :—

"Hier ist keine Spur, keine Andeutung, welche auf eine Zertheilung zu Fünf hinführen könnte. Alles wird, bis zu den geringsten Kleinigkeiten, von der

* "Descriptions of some new Fossils from the Niagara Group," Twentieth Annual Report New York State Cabinet of Natural History. Albany, 1867, p. 315.

† "Ueber Cystideen." Abhandl. d. k. Akad. d. Wiss. Berlin, 1844, p. 99.

Zahl Sechs bestimmt und beherrscht, eine Zahl, welche sich auf keine Weise mit Fünf vereinigen lässt. Der Kelchboden besteht aus vier ungleich grossen Asseln, welche, wie vorher gezeigt worden ist, sich ohne Mühe zu sechs ganz gleichen und ähnlichen Asseln zerlegen lassen. Sechs Seitenasseln, sechs Schulterblätter, bilden den Kelch, und sechs Arme erheben sich auf seinem Rande, drei doppelte nämlich und drei einfache. Das alles ist den übrigen Crinoideen ganz fremd."

Hall *, in 1852, referred to the four basals, six costals, six scapulars, and two interscapular plates of *Caryocrinus*; while Roemer † described the cup as dicyclic, with four basals, six parabasals, six radials, and two interradials, or, as we should now say, four infrabasals and six basals. It is therefore not a little surprising that Gottsche should have endeavoured to reduce the symmetry of *Caryocrinus* to that of a pentamerous type like *Actinocrinus*, from which Von Buch had so carefully distinguished it.

Few recent writers, however, seem to have understood that the cup of *Caryocrinus* is hexamerous with a dicyclic base, followed by radials, though both facts are clearly explained by Quenstedt ‡. Zittel §, for example, calls the four unequal plates which rest upon the stem the basals; but his nomenclature goes no further, though his account of the number of plates in the dorsal cup is correct enough. Steinmann ‖ also says that "Zum basalen Kranz gehören 4 Platten," which are followed by a second row of six, alternating with the plates of the first and third cycles. But then he goes on to say "Der dritte Kranz setzt sich ebenfalls aus 6, etwas niedrigeren Tafeln zusammen." He here omits all notice of the two plates which are intercalated within the ring of radials, each resting on the truncated end of a large anterolateral basal (Pl. I. fig. 2; 13, 18). The appendages of the adjacent radials encroach more or less upon these plates, which were called interscapulars by Hall, and may perhaps now be considered as true interradials, corresponding to the similarly situated plates in *Thaumatocrinus* and *Rhodocrinus*.

These eighteen plates of *Caryocrinus* reappear, plate for plate, in Von Koenen's two genera, *Corylocrinus* and *Juglandocrinus*,

* 'Palæontology of New York,' vol. ii. 1852, p. 216.
† 'Lethæa Geognostica,' Bd. i. Theil 2, 1852–54, p. 269.
‡ 'Petrefactenkunde Deutschlands,' Bd. iv. 1876, 1874–76, p. 662.
§ 'Handbuch der Palæontologie,' Bd. i. 1876–80, p. 418.
‖ 'Elemente der Paläontologie,' 1888, p. 183.

from the Caradoc beds of Montpellier. They are both dicyclic and hexamerous, though this is not the way in which Von Koenen interprets their structure *. The two genera resemble one another and differ from *Caryocrinus* in the absence of any appendages on the third cycle of plates, or radials. In *Caryocrinus* the upper edges of these plates meet the peripheral plates of the vault, the construction of which will be considered later. But in *Hemicosmites* there are no appendages round the margin of the calyx, which contains another cycle of plates above the radials. Müller † has given a good description and figure of the six plates which bound the peristome and support the three ambulacra proceeding from it (fig. I. on p. 22). I believe that these plates reappear in *Juglandocrinus* (fig. III.), a point to which we shall return.

Caryocystis granatum, as described by Von Buch ‡, also has a proximal series of two large and two small plates, which I regard as infrabasals. Above these come in succession three alternating series of six plates each, basals, radials, and interradials (in the widest sense of the term), and above these again are other plates, somewhat irregularly disposed, which are probably mere indifferent body-plates.

Gottsche's interpretation of this type is a curious one §. He regards the base as monocyclic, and five of the six plates in the next ring as R′, the odd one being an interradial, just as in *Hemicosmites*. Above these he places five second radials, altogether overlooking the fact that R″ do not alternate with R′ in any Crinoid, so that any comparison which assumes this must be altogether devoid of a morphological basis; and it is curious that the very distinct hexamerous symmetry of this type should have so entirely escaped Gottsche's notice. The form which is figured in Angelin's 'Iconographia' || under the name of *Caryocystis testudinaria* is pentamerous, while *C. alutacea*, Angelin, and *C. prominens*, Angelin, seem to be tetramerous. In like manner some forms of *Protocrinus oviformis* are distinctly dicyclic and hexamerous, while others are more irregular and indicate a divergence

* "Ueber neue Cystideen aus den Caradoc-Schichten der Gegend von Montpellier," Neues Jahrb. f. Min. 1886, Bd. ii. pp. 249–254.

† "Ueber den Bau der Echinodermen," Abhandl. d. k. Akad. d. Wiss. Berlin, 1853, Taf. vi. fig. 5.

‡ *Loc. cit.* pp. 17, 18, Taf. ii. fig. 4. § *Loc. cit.* p. 13.

|| 'Iconographia Crinoideorum,' 1878, tab. xiii. fig. 8.

towards such types as *Megacystis* and *Echinosphæra*, in which it is difficult to trace any definite symmetry, though certain individuals appear to have a hexamerous base; and the peristome of *Echinosphæra aurantium* may have two, three, or four ambulacral extensions, thus foreshadowing the variations of *Actinometra*. It may be noted, however, that Hall mentions a single species of Crinoid from the Hamilton group with a hexamerous base *. Four Cystidean genera, at any rate, *Caryocrinus*, *Corylocrinus*, *Hemicosmites*, and *Juglandocrinus*, are typically hexamerous, a point which is not without interest from its bearing on the general question of the morphology and phylogeny of the Echinoderms.

Many pentamerous Cystids resemble the types above mentioned in having a dicyclic base. Thus in *Echinoencrinus* (Pl. I. figs. 3, 4) the so-called basals, plates 1–4 of Forbes's nomenclature †, are really infrabasals, plate 3 being a double plate. Alternating with these are the subovarian series (Nos. 5–9) or first parabasals of Volborth ‡, which are the true basals; while the second parabasals or centrolaterals, Forbes (Nos. 10–14), are, I believe, the radials. The lower part of the body is constructed upon this plan in all the following genera:—*Apiocystis*, *Callocystis* (Pl. I. fig. 5), *Cystoblastus* (fig. 7), *Glyptocystis* (fig. 8), *Lepadocrinus* (fig. 6), *Pleurocystis*, *Prunocystis*, *Pseudocrinus*, and probably also in *Sphærocystis* and *Strobilocystis*; and although in some cases, *e. g. Echinoencrinus*, the radial character of these second parabasals is not apparent at first sight, yet in types like *Pseudocrinus* and *Apiocystis* they are traversed by some of the ambulacra, while in *Cystoblastus* (Pl. I. fig. 7) they are deeply incised by the latter, and are transformed into regular fork-pieces, like the radials of the Blastoids, as already noticed by Volborth §. The resemblance of all these types to one another is such that if plates 10–14 of *Cystoblastus* be admitted as radials (and this, I think, will scarcely be denied) the same name must be extended to the centrolaterals or second parabasals of all the

* 'Palæontology of New York,' vol. ii. p. 223.

† "On the Cystideæ of the Silurian Rocks of the British Islands," Mem. Geol. Survey Great Brit. 1848, vol. ii. part 2, p. 487.

‡ "Ueber die Arme der bisher zu den armlosen Crinoiden gezählten Echinoencrinen," Bull. Class. Phys.-Math. Acad. Imp. Sci. St. Pétersbourg, 1844, tome iii. No. 6, p. 2 (of separate copy).

§ "Ueber Achradocystites und Cystoblastus, zwei neue Crinoideen-Gattungen," Mém. Acad. Imp. Sci. St. Pétersbourg, 1870, tome xvi. no. 2, p. 12.

remaining genera. It will then be convenient for descriptive purposes to denote the five radials by the letters A–E, as I have done in the case of the Crinoids * and Blastoids, taking the anterior radius as A, and those to the right and left of the anus as C and D respectively †. The infrabasals, being radially situated, may then be denoted by the corresponding small letters, plates *c* and *d* being those which, in all the above-mentioned genera, are fused into the large double plate 3 (Pl. I. figs. 3–8).

Above and alternating with the radials of *Echinoencrinus* are the five plates of the fourth cycle (15–19), which Forbes called supra-ovarian, and Volborth radial axillaries. I have endeavoured to show, however, that the plates in *Echinoencrinus* which really represent the radials of other Echinoderms are the centrolaterals or second parabasals of Volborth; and these, together with the two series of plates in the dicyclic base, make up the complete dorsal cup, such as we find in many Asterids, Ophiurids, and Crinoids. But it is not easy to assign any definite homologies to the fourth series of plates in the Cystidean calyx, even supposing that they are always identical in character. In *Hemicosmites* (fig. I.) two of them are distinctly radial, and one is interradial, while the other three have no definite position. They sometimes alternate very regularly with the radials, as in *Echinoencrinus* (Pl. I. figs. 3, 4), and so would almost seem to be interradials. In certain genera one of them is missing, and not always the same one, as I shall show immediately. But even in *Echinoencrinus* there are indications of their being in relation with the divisions of the lobate peristome, and in the somewhat irregular calyx of *Glyptocystis* (Pl. I. fig. 8) each of them supports an ambulacrum, a point to which I shall return.

All the three Russian species of *Echinoencrinus* ‡ have two pore-rhombs in the base of the cup, which are situated on plates

* "On the Genus *Actinometra*, Müll., with a Morphological Account of a new Species from the Philippine Islands," Trans. Linn. Soc., Zool., 1879, vol. ii. p. 26.

† The lettering used above follows the course of the coiled gut of a Crinoid, as seen from the ventral side, and it thus goes in the reverse direction to Forbes's numbering of the Cystidean plates, as seen from the dorsal side.

‡ I have not attempted to go into the complicated question of the synonymy of this genus, but have simply made use of the names employed by Volborth in his memoir "Ueber die Echinoencrinen" (Bull. Acad. Imp. Sci. St. Pétersbourg, 1842, tome x. p. 293).

1–5 and 1–6 respectively (Pl. I. fig. 4). *E. granatum* has three other rhombs in the higher parts of the cup, while in *E. striatus* and *E. angulosus* there is but one, on plates 14–15 (Pl. I. fig. 4). This, together with that on plates 1–5, reappears in the two British species, and a third rhomb, on plates 12–18, is often present (Pl. I. fig. 3). All the species of *Pseudocrinus* have rhombs on plates 1–5 and 14–15; while in the two bifasciate species (*P. bifasciatus* and *P. magnificus*) the third or left-hand rhomb is on plates 13–17 *, its lower half being on radial D (13) instead of on radial E (12), as in *Echinoencrinus armatus* (Pl. I. fig. 3). I believe, however, that it occupies the latter position in the two quadrifasciate species, as it also does in *Apiocystis*, but the fact is not mentioned by Forbes. His figures of the two bifasciate species show that they have but four supra-ovarian plates, that of interradius AB (No. 16) being absent. It is present, however, in the other two species, or at any rate in *P. quadrifasciatus*; while in none of the specific descriptions is there any reference to a 19th plate in the cup. But in the generic diagnosis five supra-ovarian plates are described †, thus raising the total to nineteen, viz., 4, 5, 5, 5.

We meet with a similar difficulty in the case of *Apiocystis*. On p. 501 it is stated that the number and arrangement of the plates is the same as in *Pseudocrinus*. But there is no mention of any plate 19, and upon p. 502 the supra-ovarian series is described as consisting of four plates only, though five are mentioned in the generic diagnosis on p. 503. At any rate, if one be missing it is not that of the interradius AB (No. 16), which would normally rest on radials 10 and 11, and is absent in the bifasciate species of *Pseudocrinus*; for this plate is well shown in Forbes's figures 1 and 6, as also in *Pseudocrinus quadrifasciatus*. The two interradials of the left side (17, 18) are certainly present, as also the second one on the right (15), but it is not easy to make out from Forbes's figures, or indeed from the specimens, whether one is present on the anal side. According to his descriptions *Apiocystis* resembles *Echinoencrinus angulatus* in having rhombs on plates 1–5 and 14–15, and he mentions a third on plates 13–18 of the left side. I believe, however, that 13 is here a misprint

* In Forbes's diagram of *P. magnificus* the two halves of this rhomb are stated to be on plates 13–18. The latter is obviously a misprint for 17, as is apparent from the figures of the species on Forbes's plate xii.

† *Loc. cit.* p. 500.

for 12, which is nowhere noticed in Forbes's description of the cup, while he states that 13 is on the posteal side; and so far as I can judge from the specimens which I have seen, this is certainly the case.

In Hall's figures of *Apiocystis elegans* * the plate bearing the lower half of the left-hand rhomb is marked 12, and, I believe, correctly so; but I cannot agree with his interpretation of the higher plates of the cup. Resting on basals 7 and 8, and notched, like them, by the anal opening, is a plate which Hall describes as sometimes simple and sometimes divided into three †. He refers to it as belonging to the third series, and rightly so, I think; but the simple plate is marked 17 in one of his figures, and in the other its three parts are called 17, 18, and 19 respectively, which would seem to imply that it belongs to the fourth or supra-ovarian series. It appears to me, however, that this plate, whether simple or compound, is plate 13 of the centrolateral series, or, as I should call it, radial D. It touches on the left the rhombiferous plate 12, and altogether corresponds to plate 13 in Forbes's figures of *Echinoencrinus*, more especially *E. armatus*, var. (Pl. I. fig. 3). In like manner the rhombiferous plate on the right, which is marked 13 in Hall's figures, is radial C, plate 14 of Forbes's nomenclature, and I would alter the numbering of the remaining plates as follows:—

Hall.		Numbering now proposed.
A, fig. 5.	B, fig. 6.	
17	17, 18, 19	13
13	13	14
19	21	15
14	14	16
15	15	17
16	16	18
18	20	19

* 'Palæontology of New York,' vol. ii. pl. li. figs. 5, 6.

† *Ibid.* p. 242.

A similar correction should, I believe, be made in the description of *Lepadocrinus*, as given by Hall *. He states that there are four plates in the first and five in the second series, but only four in the third, Nos. 10, 11, 12, 13, the last two bearing pectinated spaces. Above these come the five supra-ovarian plates, Nos. 14–18. There is no mention of any additional plate, though 19 are shown in his figure †, which I have copied for comparison with that of *Echinoencrinus* (Pl. I. figs. 3, 6). As in the case of *Apiocrinus elegans*, it will, I think, be clear that the supra-ovarian plate which arches over the anus is No. 13, or radial D, while the rhombiferous plate to its right is really 14, and not 13 as believed by Hall. The interradial plate above this, which bears the other half of its rhomb, would then be 15, and the corresponding one on the left side 18, as I have marked in my copy of Hall's figure (Pl. I. fig. 6).

If this interpretation of the calyx be correct, *Apiocystis elegans* and *Lepadocrinus Gebhardi* resemble both *Echinoencrinus* and one another in having a complete series of five interradials, making a total of nineteen plates, with pore-rhombs on 1–5, 12–18, and 14–15. The two American species have four ambulacra, a point in which they resemble the British *Apiocystis pentremitoides*, with a similar arrangement of pore-rhombs. But it is not clear whether this last type has all five interradials, and the same may be said of the two quadrifasciate species of *Pseudocrinus*. Hall ‡ and Zittel § have included *Lepadocrinus*, *Pseudocrinus*, and *Apiocystis* under the one generic name *Lepadocrinus*, but it appears to me that the two bifasciate species of *Pseudocrinus* represent a distinct generic type for which Pearce's name should be retained. It is possible that the quadrifasciate species and also *Apiocystis pentremitoides* are congeneric with *A. elegans* and *Lepadocrinus*; but if it should ever be proved that the interradial CD is absent in the former and present in the latter, Forbes's genus might perhaps be retained, and increased by the addition of the two quadrifasciate species of *Pseudocrinus*.

The relations of these three genera would then be somewhat as follows :—

* 'Palæontology of New York,' vol. iii. p. 127.
† *Ibid.* pl. vii. fig, 23. ‡ *Ibid.* vol. iii. p. 126.
§ 'Palæontologie,' Bd. i. p. 421.

	Left-hand Rhomb.	Ambulacra.	Interradials.	
Pseudocrinus bifasciatus	13–17	2	AB missing.	*Pseudocrinus.*
„ *magnificus*	13–17	2	AB missing.	
„ *quadrifasciatus*.	12–18?	4	CD missing.	*Apiocystis.*
„ *oblongus*	12–18?	4	CD missing.	
Apiocystis pentremitoides	12–18	4	CD missing.	
„ *elegans*	12–18	4	All present.	*Lepadocrinus.*
Lepadocrinus Gebhardi.....	12–18	4	All present.	

N.B.—*Pseudocrinus*, as limited above, is probably a good genus; but I have my doubts as to the separation of *Apiocystis* from *Lepadocrinus*.

Another interesting and geologically earlier form is *Lepocrinites* (*Lepadocrinus*) *Moorei* of Meek *, from the Cincinnati group of Indiana, which differs from *L. Gebhardi* in having five ambulacra and a pore-rhomb on plates 10–15, in addition to those on 1–5, 12–18, and 14–15. I am inclined to regard these characters as of generic value, and would propose therefore to distinguish Meek's species by the name *Lepadocystis*.

Callocystis is another genus presenting the same general plan of structure, though I should not interpret its calyx quite in the same way as Hall † has done. Five of the eight costals which he describes in the second cycle are, I believe, the true basal plates, Nos. 5–9 (Pl. I. fig. 5), those namely which are marked 5, 6, 8, 9, 11 in Hall's figure; while his plates 7, 10, and 12 seem to me to represent radials E, C, and B, or plates 12, 14, and 10 respectively, in *Echinoencrinus* and *Lepadocrinus* (Pl. I. figs. 3, 6). They are situated lower than usual and enter the basal ring, just as the posterior radials do in certain species of *Hemicidaris* and other Urchins. The anal opening would then be situated between basals 7 and 8 below and a single plate above, which I regard as representing radial D or plate 13 of *Echinoencrinus* and *Lepadocrinus* (Pl. I. figs. 3, 5, 6). This being the case, the pore-rhombs of *Callocystis* occupy the same positions as those of the above-mentioned types, viz., on plates 1–5, 12–18, and 14–15, though its five ambulacra and the peculiar relations of its radials give it a very distinct generic position.

* Rep. Geol. Surv. Ohio, Palæontology, vol. i. 1873, p. 39, pl. iii. fig. 4.

† 'Palæontology of New York,' vol. ii. p. 238, pl. l.

White * has described a Devonian genus, *Strobilocystis*, in which "the principal plates are probably similar to those of *Callocystis*." It has three pairs of rhombs, but only four ambulacra. Its generic position must, therefore, remain uncertain till the composition of its calyx can be definitely ascertained.

We have seen that in the bifasciate *Pseudocrinus* the interradial AB is undeveloped, while in *Apiocystis* that of CD is perhaps wanting. *Cystoblastus* is distinguished by the absence of any plate in interradius DE, the suture between these radials being continued right up to the peristome, just as in many Blastoids (Pl. I. fig. 7). This type is further remarkable for the entry of the other four interradials into the radial ring, two of them (17, 18) appearing in the figure. In fact, No. 18 forms the right-hand margin of the anal aperture, and cuts plate 14 off from it altogether. It may be noted too that in *Cystoblastus*, as in the Russian species of *Echinoencrinus* (Pl. I. fig. 4), there is a pore-rhomb on plates 1–6 in addition to that on 1–5, as Volborth † and Schmidt ‡ have already pointed out.

Another remarkable form with the same two basal rhombs and largely developed interradials (?) is the *Glyptocystis multipora* of Billings § (Pl. I. fig. 8). Plates 16 and 17 are both of unusual size, the former coming down to rest on basal 5, so as to separate radials 10 and 11, which last is a small plate, just as in *Callocystis* (fig. 5); while No. 12 is also much reduced, and plate 7 is altogether to the left of the anus, which is bounded by basal 8 and radials 13, 14, as it would be in *Cystoblastus*, but for the low position of interradial 18 (Pl. I. fig. 7). On the other hand, in the Russian *Glyptocystis pennigera*, the anal opening is greatly extended at the expense of two basals (7, 8) and three radials (12, 13, 14), and was covered, according to Schmidt||, by a delicate plated integument. From such a form as this the transition is

* "Descriptions of New Fossils from Palæozoic Rocks of Iowa," Proc. Acad. Nat. Sci. Philad. 1876, p. 28.

† Mém. Acad. Sci. St. Pétersbourg, 1870, tome xvi. no. 2, p. 12.

‡ "Ueber einige neue und wenig bekannte Baltisch-Silurische Petrefacten," *ibid.* 1874, tome xxi. no. 11, p. 10.

§ "On the Cystideæ of the Lower Silurian Rocks of Canada," Figures and Descriptions of Canadian Organic Remains, decade iii. 1858, p. 54, pl. iii.

|| *Loc. cit.* p. 18, tab. i. figs. 7 *d*, 10. [N.B.—Schmidt's numbering goes from right to left across the page; while that of Forbes, which I have followed, goes from left to right. If Schmidt's figures be altered in accordance with this plan, basal 9, beneath the anus, becomes basal 7, as I have implied above.]

easy to *Pleurocystis*, Billings, in which basals 7 and 8 and radial 13 seem to be altogether lost in the integument of small plates covering the anal side. Compare, for example, figs. 1 *a* and 1 *c* on plate i., or figs. 1 *a* and 1 *b* on plate ii. of Billings's memoir *, with figs. 7 *a* and 7 *d* on Schmidt's tab. i. On the other hand, the numerous pore-rhombs of *Glyptocystis* are reduced to three in *Pleurocystis*, which are situated respectively on plates 1–5, 13–14, and 11–12, the first of which is, as we have seen, common to all this group of Cystids.

There is one point about *Glyptocystis* which cannot be left without notice, and I must confess that it has puzzled me a good deal, viz., the relations of the ambulacra to the calyx-plates. In the case of *Cystoblastus* (Pl. I. fig. 7) the five plates which a morphological study of the abactinal pole indicates as the radials also stand in direct relation to the ambulacra, so that there can be no possible doubt about their homology. *Apiocystis* and *Lepadocrinus* have but four ambulacra, which sometimes extend down on to the basals, as in *Hybocystis*, and two or more of the radials are traversed by the ambulacra, the relations of which to plates 10 and 11 (radials A and B) are well seen in Hall's figures of *Apiocystis elegans* † and *Lepadocrinus Gebhardi* ‡. But in *Glyptocystis multipora*, with its somewhat irregular calyx, this is much less evident (Pl. I. fig. 8). Plates 12, 13, and 14 are all traversed by ambulacra; but that corresponding to plate 10 is too short to reach it, while the remaining one lies altogether to the left of plate 11, and passes at once from plate 16 on to the basal below it. On the other hand, the five plates (15–19) which lie above the radials of this type, alternating with some of them, and resting directly upon others, seem to coincide in position with the ambulacra (Pl. I. fig. 8). This is still more marked in the Russian species, *G. pennigera*, and especially in *G. sculpta* and *G. gigantea* §, in which the fourth series of plates have almost the same relation to the ambulacra as those of the aberrant Blastoid *Cryptoschisma*. A somewhat similar condition appears in *Lepadocystis Moorei*, and under these circumstances it is not easy to assign any definite homologies to these plates of the fourth series in the Cystidean calyx. They are occasionally

* *Loc. cit.*

† 'Palæontology of New York,' vol. ii. pl. li. figs. 1–4.

‡ *Ibid.* vol. iii. pl. vii. figs. 2, 4.

§ Mém. Acad. Imp. Sci. St. Pétersbourg, 1874, tome xxi. no. 11, tab. ii. figs. 9, 11.

altogether absent, as in *Hybocystis*, and although apparently interradial in position in some types, they seem in others to be definitely related to the ambulacra. They would probably be best considered as perisomic plates, without any distinct orientation; and in some forms they are succeeded by others of the same character. Such, for example, are the small plates round the peristome of *Cryptocrinus* and *Apiocystis elegans*, and the larger ones of *Glyptocystis pennigera*; while in many Cystideans the whole body is made up of these irregularly arranged perisomic plates, just as in the Psolidæ among the Holothurians, and all traces of a calyx comparable to that of a Crinoid have disappeared.

Under the name of *Caryocystis pumila*, Eichwald * has figured a curious form with the body covered by four, or perhaps five, alternating series of plates. The anus is low down, notching two of the plates of the second series, which I take to be the basals, just as in *Hemicosmites*, *Echinoencrinus*, and their allies (Pl. I. figs. 1–6). In the rare genus *Prunocystis* † from Dudley there are at least three regular alternating series of plates, which correspond respectively to the infrabasals, basals, and radials of *Echinoencrinus*. The same is the case in *Macrocystella* ‡, Callaway, of Tremadoc age, and also in another member of the Primordial fauna, *Lichenoides*, Barrande §. Two others of Barrande's genera, *Mimocystis* and *Homocystis*, present similar characters ||, and would seem, indeed, to belong to the same group as *Echinoencrinus*, as already suggested by Barrande, but they are not sufficiently well preserved for this to be made out with certainty.

Enough has been said, however, to show that there are a considerable number of Cystids which are characterized by the possession of a dicyclic calyx like that of a Crinoid, and that these may be grouped round two central forms, *Caryocrinus*, with hexamerous symmetry, and *Echinoencrinus*, which is penta-

* 'Lethæa Rossica,' 1860, vol. i. sect. 1, p. 629, pl. xxxii. fig. 19 *b*.

† Mem. Geol. Survey, vol. ii. pt. 2, pl. xvi.

‡ "On a new Area of Upper Cambrian Rocks in South Shropshire, with a Description of a new Fauna," Quart. Journ. Geol. Soc. 1877, vol. xxxiii. p. 669, pl. xxiv. fig. 13.

§ 'Système Silurien du Centre de la Bohême,' vol. vii. 1887, Cystidées, p. 183, pl. i.

|| *Ibid.* pp. 77, 160, 164, pl. xxviii.

merous, with the two infrabasals of the anal side (CD) united into one large plate. *Echinoencrinus* and *Caryocrinus* are taken by Steinmann * as the types of his group Cystocrinoidea, while *Lepadocrinus*, which he unites with *Pseudocrinus*, is placed with *Glyptosphæra* and *Echinosphæra* among the Eucystoidea, in which there are "keine deutlichen freien Arme, dagegen meist Ambulacralfurchen oder -felder entwickelt." Steinmann does not state his views respecting *Callocystis* and *Apiocystis*; but I cannot see that their appendages, or those of *Lepadocrinus* and *Pseudocrinus*, are in any way so markedly different from those of *Echinoencrinus* as to justify a separation of this kind. The ambulacra of *Echinoencrinus* are very short, and hardly extend beyond the peristome, so that the appendages are limited to its immediate neighbourhood, forming what Steinmann calls "freie Arme an der Grenze der Ober- und Unterseite." But *Lepadocystis Moorei* and *Lepadocrinus Gebhardi*, together with *Apiocystis* and *Callocystis*, afford a complete transition to the condition of *Pseudocrinus*; and considering the resemblance in the composition of their dorsal cups, I should include all these genera in the Cystocrinoidea, leaving the more irregular forms with numerous plates as the Eucystoidea.

We have seen that one of the infrabasals in the pentamerous *Echinoencrinus*-group is a double plate (Pl. I. figs. 3–8; 3), and that there are two such plates in the hexamerous *Caryocrinus* and its allies (Pl. I. figs. 1, 2). This is also the case in the pentamerous *Hypocrinus* and *Cryptocrinus*. In both types, so far as I can make out from the published figures of them, the single infrabasal is that of the right anterior ray (B), those of radii AE and CD being respectively fused (Pl. I. fig. 9).

Hypocrinus † is certainly a very singular form, and one would like to know more about it. The three infrabasals are followed by five equal and similar basals, and these again by five radials which are described by Beyrich as bearing "die Ansatzstellen der Arme." The anal opening is placed at the top of one of the basals, also notching the lower angles of the two radials which rest upon it, a condition which recalls that of *Gasterocoma* among the Crinoids. *Glyptocystis multipora* presents a similar peculiarity (Pl. I. fig. 8), and the same would be the case in *Cystoblastus*

* *Op. cit.* p. 182.

† See Beyrich, "Ueber eine Kohlenkalk-Fauna von Timor," Abhandl. d. k Akad. d. Wiss. Berlin, 1864, p. 83, Taf. ii. fig. 16.

(Pl. I. fig. 7), but for the intercalation of an interradial plate (18) within the radial ring. Beyrich was inclined to refer *Hypocrinus* to the Cystids, chiefly, it would seem, on account of this character, and his example has been very generally followed. But it is altogether unlike the other Carboniferous Cystids, and I cannot help suspecting that it is really a Crinoid, allied to *Lecythiocrinus*, White *. The type-specimen of this genus, which was found in the Upper Coal Measures of Kansas, has three infrabasals, two of which are double plates, just as in *Hypocrinus*; and above these are five basals and five radials, the latter being bent inwards, somewhat as in *Hypocrinus*, and bearing small facets for the arms. In this species, *L. olliculæformis*, there is no trace of an anal aperture in the dorsal cup, and it would seem, therefore, to have been situated in the disk above. But in the unique *L. Adamsi*, Worthen †, from the lower Coal Measures of Illinois, which has five infrabasals, there is a circular opening between the summit of one basal and the lower angles of the two radials above it. Worthen described this as filled with stony matter, and left it an open question whether it is "an anal opening or an accidental break in the test of the body." The analogy of *Hypocrinus* would seem to indicate that this is an anal opening, and that *L. Adamsi* should be referred to this genus and not placed with *L. olliculæformis*, in which the anus does not open within the dorsal cup. The latter is also the case in the Devonian genus *Codiacrinus*, Schultze, which likewise has three infrabasals, five basals, and five radials, all in contact; and except in the characters of the arm-facets, there is no structural difference between *Lecythiocrinus*, as defined by White, and Schultze's type. Wachsmuth and Springer have noticed this resemblance ‡; but they say nothing about Worthen's remark as to the possibility of the anus piercing the dorsal cup of *L. Adamsi*. Should this really be the case, this species can hardly be referred to White's genus; while, except in the number of infrabasals, it would much resemble *Hypocrinus*, to which Wachsmuth and Springer make no reference in the text of the 'Revision,' though the name appears in the index. They might have known

* "Descriptions of New Species of Carboniferous Invertebrate Fossils," Proc. U.S. Nat. Mus. 1880, vol. ii. p. 256, pl. i. figs. 4, 5.

† Geol. Survey of Illinois, vol. vii. 1883, p. 317, pl. xxx. fig. 8.

‡ "Revision of the Palæocrinoidea.—Part III. Sect. 2," Proc. Acad. Nat. Sci. Philad. 1886, p. 152.

that Beyrich's genus is figured in the atlas to Quenstedt's Encriniden, though the type is described in the text as a Cystid*. S. A. Miller† has proposed to replace *Lecythiocrinus*, White, by *Menocrinus*, on the ground that the former name is pre-occupied by *Lecythocrinus* of Müller and Zittel. But the two names are not identical; and even if they were, there is some doubt as to the validity of Müller's genus, so that there is no need for the introduction of *Menocrinus*. Miller‡ notices the difference between the two American species in the number of infrabasals, though he persists in calling them basals, and he regards it, if really existing, as of generic value; but he appears never to have heard of *Codiacrinus* and *Hypocrinus*. The similarity of the plates in the dorsal cup in the latter type to those of *Codiacrinus* and *Lecythiocrinus* seems to me to indicate clearly that it is a Crinoid and not a Cystid. The same view has been taken by Bather§.

Cryptocrinus is also a very puzzling form (Pl. I. fig. 9). I have endeavoured to reconstruct the calyx of *C. cerasus* from Von Buch's projection‖, which does not seem to be altogether in accordance with his description or other figures. He supposed that one of the five plates (*Seitenasseln*) which rest upon the three infrabasals was divided horizontally into two parts, which I have marked respectively 7 and 13. The five plates above these (*Scheitelasseln*, Von Buch) would then come to be radials. His projection shows an additional plate between 9 and 10, which is not at all clear in his two views of the cup from above and the side. I have indicated it in fig. 9 by a dotted line, and have marked it *x*. It would seem to belong to the peristomial series rather than to that of the dorsal cup, and may be left out of consideration for the present. I am inclined to think, however, that plate 13 is not the upper half of a divided basal, as supposed by Von Buch, but that it should rather be regarded as radial D, which has been displaced downwards and a little to the side, so as to rest directly on basal 7, and underlie radials 12 and 14 (E and C). The analysis of the calyx of *Cryptocrinus lævis* which

* *Op. cit.* p. 687, tab. 113. fig. 94.

† 'North American Geology and Palæontology,' 1889, p. 262.

‡ "The Structure, Classification, and Arrangement of American Palæozoic Crinoids into Families," Amer. Geologist, 1890, vol. vi. p. 351.

§ "British Fossil Crinoids, II.," Ann. & Mag. Nat. Hist. 1890, vol. v. p. 382.

‖ *Loc. cit.* Taf. ii. fig. 5.

appears in Angelin's 'Iconographia' * may be interpreted in the same way, and the small peristomial plates which appear to belong to the ambulacral skeleton are well seen in his figures of the summit †. One of the latter also shows the low pyramid of five oral plates, one of which is considerably larger than its fellows. The large one, however, is not that of the anal interradius (CD) as in *Sphæronis*, but that of the next one (DE), in which the so-called genital opening is placed.

In the preceding pages I have endeavoured to show that many Cystideans have a calycular system which is essentially similar to that of the Crinoids, and I cannot, therefore, agree with Lovén ‡ when he says:—"In the Cystoidea—in which every trace of a calyx is wanting, at least in the adult—the basal part of the skeleton is formed by the perisome alone." This seems to me to be far too general a statement, though it is no doubt applicable to *Sphæronis*, *Glyptosphæra*, and similar forms. But I can scarcely imagine that Lovén will deny the presence of a calyx in such forms as *Cystoblastus* (Pl. I. fig. 7), or even in *Caryocrinus* (fig. 2), though he appears to believe this to be the case in *Callocystis* (fig. 5).

2. The Summit Openings.

Most palæontologists now believe that the mouth of a Cystid was placed at the point of convergence of the ambulacra, as is the case in all the other Echinoderms, and the anal function of the lateral valvular opening has been generally acknowledged for some time past, as may be seen in any standard text-book of zoology and palæontology, though Sturtz § has recently suggested that it may represent the madreporic opening of Starfishes. Under these circumstances it is not a little unfortunate that the whole question should again have been thrown into confusion by S. A. Miller, whose utterances on the subject of Cystids in his recent volume on North American Geology and Palæontology are vague in the extreme. He admits that the mouth of a Blastoid was situated at the point of convergence of the ambulacra, and that the lateral opening was the anus. In his diagnoses of *Glyptocystis* and *Gomphocystis*, however, he calls the latter the

* *Op. cit.* tab. xii. fig. 2. † *Ibid.* figs. 3–5.

‡ "On *Pourtalesia*, a Genus of Echinoidea," K. Svensk. Vetensk. Akad. Handl. 1883, Bd. xix. No. 7, p. 10.

§ "Neuer Beitrag zur Kenntniss palæozoischer Seesterne," Palæontographica, Bd. xxxvi. 1890, p. 242.

mouth and the former the ambulacral opening, though he never explains the meaning of this term. His descriptions of *Agelacrinus* and *Apiocystis* contain no reference to the mouth at all; but the lateral valvular opening, which is called the mouth in *Glyptocystis*, is noticed as ovarian in *Apiocystis*, and as ovarian or anal in *Agelacrinus*, while in the case of *Caryocrinus* it is spoken of as "the mouth or anal orifice" *. From Miller's descriptions of *Callocystis*, *Hemicosmites*, and *Sphærocystis*, it may perhaps be inferred by a "scientist" that he believes the mouth of these types to be situated at the ambulacral centre. But the average amateur or student, for whom the book is also published, could hardly be expected to discover this fact from such statements as "oral, ovarian, and anal apertures," or "mouth apical; opening subapical; ovarian opening on the summit" †.

No educated palæontologist would now admit the possibility of such extraordinary departures from the general type of Echinoderm structure as Miller's descriptions involve; and few, if any, will now deny that the position of the mouth of a Cystid coincides with that of the ambulacral centre, as was so ably argued by the late Sir Wyville Thomson ‡ in 1861, and subsequently by Lütken § and A. Agassiz ‖. In some genera there is evidence of its having been concealed beneath a covering of oral plates, as in so many Palæocrinoids. These are well preserved in *Cyathocystis Plautinæ*, Schmidt ¶, and are tolerably equal in size, as in *Stephanocrinus*. But in various species of *Sphæronis* as figured by Angelin, in *Glyptosphæra Leuchtenbergi* (Pl. I. fig. 15), and in *Pyrocystis desiderata*, Barrande (Pl. I. fig. 11), the posterior oral is larger than its fellows, as in *Haplocrinus* and in so many Camerata **.

* *Op. cit.* p. 231. † *Ibid.* pp. 230, 282.

‡ "On a new Palæozoic Group of Echinodermata," Edinburgh New Philosophical Journal, 1861, vol. xiii. p. 112.

§ "Endnu et Par Ord om de gamle Söliliers 'Snabel' og Mund," Vid. Med. Naturhisk. Forening i Kjöbenhavn for 1869, Nr. 9–13, pp. 185–188.

‖ "Note on Lovén's Article on *Leskia mirabilis*, Gray," Annals Lyc. Nat. Hist. 1869, vol. ix. pp. 242–245.

¶ "Ueber *Cyathocystis Plautinæ*, eine neue Cystideenform aus Reval," Verh. russ. kais. min. Gesellsch. St. Petersburg, 1880, ser. 2, vol. xv. pp. 1–7.

** I take this opportunity of cordially acknowledging the generous manner in which Messrs. Wachsmuth and Springer have recently admitted the truth of the view which I have advocated persistently since 1879, respecting the homology of the four anterior proximals of the Palæocrinoidea with the orals of the Neocrinoidea. They were steadily opposed to it from the first, but have at last assented to it (Proc. Acad. Nat. Sci. Philad. 1888, p. 348); and now that they

A still closer approach to the condition of the Actinocrinidæ is presented by *Caryocrinus* (Pl. I. fig. 14). The greater part of the summit is occupied by six oral plates, together with two smaller ones, which bound the anal opening. Immediately in front of this is a heptagonal or hexagonal plate, round which the five others are grouped symmetrically. I have seen one specimen in which this plate is nearly pentagonal; and the two antero-lateral orals meet above it, pushing the anterior one away with it, so that the summit looks very much like that of an ordinary pentamerous form. The normal arrangement of these summit-plates in *Caryocrinus* at once recalls the five orals of the Camerata, viz., a central plate in front of the anus, with four others round it, the so-called proximals. But why are there five proximals in *Caryocrinus*? Simply because the symmetry of this type is hexamerous and not pentamerous. Wachsmuth and Springer must have overlooked this well-known fact when they stated that the eight plates round the central piece of *Caryocrinus* "are arranged in a totally different manner from the so-called proximals of the Palæocrinoidea"*. The anterior and the postero-lateral orals coincide in position with the primary ambulacra, of which there are only three, and they are therefore considered as radial in position by Wachsmuth and Springer, who remark:—"We think the distribution and arrangement of the surrounding plates in *Caryocrinus* prove conclusively that these cannot be orals, for the most ingenious speculator would be unable to reconstruct

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have discovered for themselves that the supposed central plate is really the displaced posterior oral, which is not represented by two small plates separated by the anus, as we formerly supposed, my comparison of it to the dorsocentral of the abactinal system need not be further considered. It is proper for me to state, however, that some months before Messrs. Wachsmuth and Springer's change of opinion had been made public, Professor Beyrich had convinced me, during a visit to Berlin at Easter, 1888, that the supposed central plate in the summit of the Camerata is really the posterior oral homologous with that of *Haplocrinus*. He had then held this view for some time, and it had been suggested as a possible one by Wachsmuth and Springer in 1885. But it was never seriously advocated by them; and even as late as 1887 they criticized me somewhat severely for still believing in the oral nature of the summit-plates in *Allagecrinus*, *Coccocrinus*, *Culicocrinus*, &c., and of the four anterior proximals in the Camerata generally. These criticisms, however, were altogether withdrawn in the following year, and we are now in complete accordance upon this long-discussed question.

* "The Summit-Plates in Blastoids, Crinoids, and Cystids, and their Morphological Relations," Proc. Acad. Nat. Sci. Philad. 1887 p. 100.

five primitive plates from such an assemblage of pieces as we find in *Caryocrinus* and in Von Koenen's new genus *Juglandocrinus*. What those plates may be, whether actinal or abactinal structures, we will not pretend to decide; but we do undertake to say that they are not orals, otherwise the rule that there are always five primitive orals meets with a very serious exception" *. I am not aware of the absolute rule to which they refer, for where there are six basals, a point which Wachsmuth and Springer have overlooked, one would certainly expect to find six orals. They have also forgotten the fact that, besides the ordinary pentamerous form of *Rhizocrinus*, Sars † described individuals with 4, 6, and 7 rays, and a corresponding number of "valvules orales."

In this same communication, published in 1887, before their change of opinion, Wachsmuth and Springer say "*Caryocrinus* has a large central piece, and this is surrounded usually by eight plates, which are arranged in a totally different manner from the so-called proximals of the Palæocrinoidea. Three of them are radial, the others are interradial. The interradial pieces alternate with the radial ones, one to each side, except at the anal interradius, where three smaller pieces take the place of the single one at the two other sides." At that time the American authors regarded the central piece as a composite oral plate, like that of the Camerata; but they have since recognized that the latter is really the posterior oral displaced forwards ‡, and that the smaller plates between it and the anus are not members of the proximal series at all, but anal plates. On the same principle *Caryocrinus* would have to be regarded as having six orals, a central one and five others round it (fig. II., and Pl. I. fig. 14). But Wachsmuth and Springer have given no hint that they now take this view of its structure, and I conclude, therefore, that they regard the summit of *Caryocrinus* as composed of three orals, a central and two antero-laterals, with three alternating radial plates which cover the ambulacra. This would mean, of course, that the actinal plates of *Caryocrinus* are trimerous and not hexamerous, as those of the dorsal cup are; and the fact that three of them cover the primary ambulacra seems, at first sight, to be a strong

* *Ibid.* p. 107.

† 'Mémoires pour servir à la Connaissance des Crinoïdes vivants,' Christiania, 1868, pp. 18, 19.

‡ "Discovery of the Ventral Structure of *Taxocrinus* and *Haplocrinus*, and consequent modifications in the Classification of the Crinoidea," Proc. Acad. Nat. Sci. Philad. 1888, pp. 342, 348.

argument in favour of this view. But the number of the ambulacra in a Crinoid or Cystid is not a satisfactory test for determining the primary symmetry of the type. A similar condition to that of the hexamerous *Caryocrinus* with three primary ambulacra is presented by the ten-rayed *Promachocrinus*, the disk of which has only five primary ambulacra. In *Actinometra*, which has a pentamerous calyx, the number of ambulacra joining the peristome may vary from three to ten, and those of the posterior rays do not by any means coincide in position with the radial plates of the dorsal side. In *Echinosphæra aurantium* there may be two, three, or four ambulacra *. *Pseudocrinus* has but two, though its dorsal cup is pentamerous, and the latter is also the case in *Sphærocystis*, *Apiocystis*, or *Lepadocrinus*, which have but four primary ambulacra. The hexamerous *Hemicosmites* has a triradiate peristomial area, while *Juglandocrinus*, also hexamerous, has three pairs of ambulacral openings; the symmetry of the ambulacra thus indicated is in each case the same as in *Caryocrinus* (figs. I.–III.). Wachsmuth and Springer have pointed out how in the latter genus the three primary ambulacra coincide in position with three of the six summit-plates, the anterior and the two postero-lateral ones. I have indicated the course of these subtegminal ambulacra in a figure of the summit, which shows the interradial position of the six orals (*o*), as determined by the symmetry of the dorsal cup (fig. II.). Since there are only three primary ambulacra which supply three pairs of radials (11–12, 14–15, 16–17), it is obvious that they would naturally occupy interradial positions and so come to lie beneath three of the orals, which were not movable like those of Neocrinoids, but formed part of a rigid tegmen. This is well shown in fig. II. (See Postscript, *infrà*, p. 51.)

In *Juglandocrinus* the ambulacra are subtegminal, but Von Koenen's description † shows clearly that there must be three primary trunks, each opening externally by two pores on the edges of the plates which he marks *m* (fig. III.). Von Koenen says in reference to these openings:—

"Sehr eigenthümlich sind bei unserer Art die sechs paarig angeordneten Löcher im Scheitel. Falls sie nicht, wie bei den Palæocrinoiden, auf Arm-Ansätze zu deuten sind, was bei ihrer Lage wenig wahrscheinlich ist, würde eine

* See Volborth, "Ueber die russischen Sphaeroniten," Verh. min. Ges. St. Petersburg, 1845–46, p. 18 (of separate copy), and Taf. ix. figs. 6-8.

† *Loc. cit.* p. 253.

Fig. I.

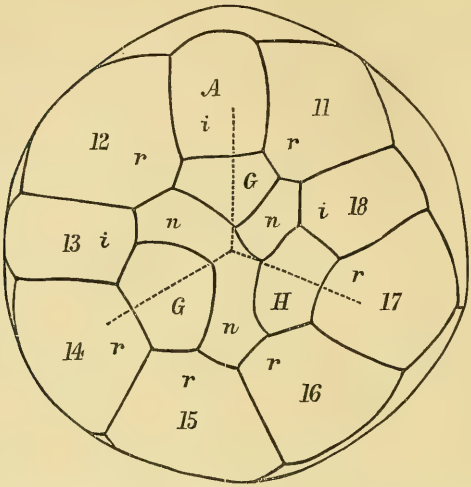


Diagram of the summit of *Hemicosmites pyriformis*. The course of the ambulacra, which are superficial, is indicated by dotted lines.—*r* (11, 12, 14–17), radial plates; A, the anterior interradial; *i* (13, 18), anterolateral interradials; G, H, *n*, peristomial plates (orals?). Copied from Müller (Abhandl. Berlin Akad. 1853, Taf. vi. fig. 5).

Fig. II.

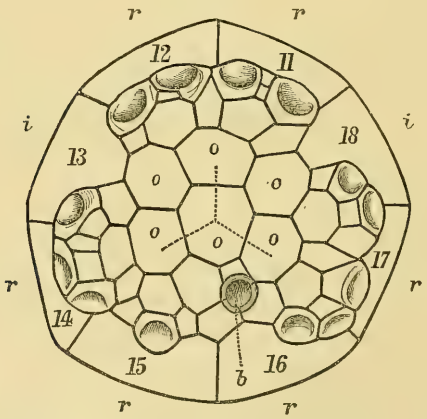
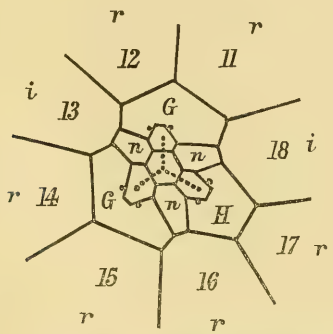


Diagram of the summit of *Caryocrinus ornatus*, showing the relation of the orals (*o*) to the plates of the dorsal cup (11–18), which are lettered as in Fig. I.—*b*, anus. The dotted lines indicate the course of the subtegminal ambulacra. From Mr. Wachsmuth's specimen, represented in Plate I. fig. 14.

sehr auffällige Analogie mit den paarigen Oeffnungen oder vielmehr Kanälen im Scheitel der Blastoideen ins Auge zu fassen sein. Sie müssen aber auch zum Theil die Funktionen von Mund und After erfüllt haben."

It seems to me that there can be little doubt as to the ambulacral nature of these six openings in the summit of *Juglandocrinus*. They were not related to hydrospires, as Von Koenen seems to

Fig. III.



Summit of *Juglandocrinus crassus*. Copied from Von Koenen (N. Jahrb. f. Mineralogie &c. 1886, Bd. ii. Taf. ix. fig. 3). The dotted lines indicate the course of the subtegminal ambulacra, which opened externally by three pairs of pores. (N.B. One of these pairs has been accidentally omitted in Von Koenen's original figure, in which the three superambulacral plates are marked *m*).—Plates 11–18, radials and interradials of the dorsal cup as in Figs. I., II.; G, H, *n*, peristomial plates (orals ?).

suggest; but the food-particles entered through them on their way to the central mouth, just as they did at the arm-openings of the Palæocrinoidea. If the comparisons drawn above between the ambulacra of *Juglandocrinus* and those of *Caryocrinus* and *Hemicosmites* be in any way valid, then the anus of the former type should be looked for somewhere in the neighbourhood of plates 15 and 16. It would also seem to follow that the central plate and the three super-ambulacral orals of *Caryocrinus* correspond respectively to the central plate and the three plates *m* of *Juglandocrinus*. I have some doubt *, however, as to whether

* One possible view would be to regard the two anterior plates, *n*, which rest upon the two interradials 13, 18, as representing the anterolateral orals of *Caryocrinus*, and the posterior plate *n* as an anal summit-plate. But if the central plate could be disestablished, as that of *Haplocrinus* was, there would then be but six plates (orals ?) in the summit, just as in *Hemicosmites* (fig. I.).

the two remaining orals of *Caryocrinus* are represented in the latter type (fig. III.), which seems to occupy a curiously intermediate position between *Caryocrinus* and *Hemicosmites*. Alternating with the three plates *m* are three others, situated interradially or nearly so, which are marked *n* in Von Koenen's figure; and outside these again, in the direction of the ambulacra, are three larger plates, two of which, G, G, are interradial, while the third, H, rests directly on the top of radial 17. These six plates are well shown in the summit of *Hemicosmites*, as figured by Müller *, and I have lettered them accordingly in my copy of his figure (fig. I.). Two points, however, are noteworthy. *Hemicosmites* has an anterior interradial, A, between radials 11 and 12, which is not represented in *Caryocrinus* or *Juglandocrinus*; and the anterior summit-plate, G, thus rests directly upon it instead of on the suture between the two radials. In the second place, the ambulacra of *Hemicosmites* are external. There is a triradiate peristome in the centre of the summit which extends outwards as grooves on to the surface of plates G, G, H, the whole structure being roofed in by smaller plates, which are probably ambulacral covering-plates, very much as in *Cyathocrinus*.

The close agreement between the varying conditions of the oral plates in different Cystidean genera and those of the later Crinoids is very remarkable. We have already traced the resemblance between the summit of *Caryocrinus* and that of an Actinocrinoid. The five orals of *Cyathocystis*, with their distal angles abutting on the ambulacral skeleton of each ray, reappear under similar conditions in the young *Platycrinus symmetricus*, recently figured by Wachsmuth and Springer †. So far as can be judged from the condition of the fossils, the orals were movable in *Cryptocrinus*, *Sphæronis*, and *Glyptosphæra* (Pl. I. fig. 15), which were the forerunners of the recent *Hyocrinus*, *Rhizocrinus*, and *Thaumatocrinus*. Lastly, in *Ascocystis* the orals, if ever developed, must have disappeared as completely as in a recent *Pentacrinus* or *Comatula*. Barrande seems to have been somewhat puzzled by the condition of the ventral surface with its five reniform compartments ‡, and believed "que l'ouverture était rameuse et composée d'arcs entourant les compartiments réniformes, d'une manière comparable à celle que nous voyons dans divers autres genres de Cystidées,

* Abhandl. d. k. Akad. d. Wiss. Berlin, 1853, Taf. vi. figs. 4, 5.

† Proc. Acad. Nat. Sci. Philad. 1888, pl. xviii. fig. 15.

‡ *Op. cit.* p. 117, pl. xxxiii. fig. 13.

comme *Echinoencrinus Senkenbergi*, Von Buch." It is obvious, however, that these ramifying lines indicate the positions of the ambulacra diverging from a central peristome, and that the five compartments which they enclose represent the five interambulacral areas on the disk of a Neocrinoid, the larger one being that of the anal interradius. It was probably pierced by the rectum, as in the recent forms, and the whole disk of *Ascocystis*, with its ambulacra dividing to supply the numerous appendages round its edge, bears a singular resemblance to that of a *Metacrinus* such as *M. nobilis* * and *M. rotundus* †, in which the pinnule-ambulacra appear on the disk. In the Pentacrinidæ, too, the peristome and the bases of the ambulacra are roofed in by covering-plates without any distinct traces of orals, just as in many Cystids.

The presence of an oral pyramid consisting of five plates in the form which Barrande called *Pyrocystis desiderata* ‡ is a point of some importance, as it conclusively settles the nature of the structures which he called "hydrophores palmés." They are well shown in his figure of the interior of the test of this type (Pl. I. fig. 10); while that of the exterior shows their relation to the oral plates, which suggests at once that they are subtegminal ambulacra. This obvious explanation of them has already been given by Neumayr on quite different grounds §; but it did not find favour with the anonymous reviewer of Barrande's work in 'Nature,' who criticised it as follows ‖ :—

"Neumayr thinks that the opening which they surround is the mouth, and that they are subtegminal ambulacral grooves. How this can be when their distal ends are unconnected with the exterior is not easy to understand. Barrande, moreover, cannot say whether they are at the oral or aboral pole. A comparison of figs. 28 and 32 on pl. xxix. suggests that they are at the aboral end, and that the large opening represents the axial canal of the stem. May they not be connected with nerve-cords passing from a chambered organ?"

The reviewer is no doubt right in assuming that the large opening seen in fig. 28 is the axial canal of the stem; but there is not much resemblance between this and the low quinquepartite pyramid of fig. 32 on the same plate, which, as shown in fig. 33

* Zool. Chall. Exp., "Report on the Crinoidea," vol. xi. 1885, pl. xliii. fig. 3.
† Trans. Linn. Soc. 1884, ser. 2, Zool. vol. ii. pl. l. fig. 2.
‡ *Op. cit.* pl. xxix. figs. 32, 33.
§ 'Die Stämme des Thierreiches,' Bd. i. 1889, p. 409.
‖ 'Nature,' vol. xl. 1889, p. 269.

(Pl. I. figs. 10, 11), covers the point of convergence of the hydrophores. This covering, however, is closely similar to what is universally recognized as the oral pyramid of *Glyptosphæra Leuchtenbergi* (Pl. I. fig. 15), a point which the reviewer must surely have forgotten, or he would scarcely have put forward the suggestion contained in the paragraph quoted above. It is singular, too, that he should not have been struck by the resemblance between the grouping of the hydrospires round a central pentagonal space and the ambulacra diverging from the angles of the low oral pyramid in *Glyptosphæra* (Pl. I. fig. 15) or in *Sphæronis*, as shown in figures 18 and 20 on pl. xi. of Angelin's 'Iconographia.' It is also somewhat remarkable that neither Barrande nor his reviewer should have noticed the resemblance of the "hydrophores" in *Pyrocystis* to the ambulacra of *Proteocystis*, which are figured and rightly interpreted on the next plate of Barrrande's monograph. A glance at this ought to have dispelled all the reviewer's doubts as to the "hydrophores" belonging to the oral pole.

Barrande would also seem to have forgotten the closure of the mouth by oral plates in *Sphæronis*, *Glyptosphæra*, and *Cyathocystis*, or he would scarcely have written of it as follows *:—"Cette ouverture n'est accompagnée d'aucun appareil destiné à la fermer. Nous devons donc concevoir qu'elle était constamment ouverte." On the following page he adopted Von Buch's opinion that the large lateral opening is genital in function and the small one near it anal; and yet the 'Nature' reviewer says that "the accepted views are confirmed by Barrande." He also compared the fourth and slit-like aperture close to the mouth of *Aristocystis* (Pl. I. figs. 12, 13, *d*) to the peculiar folded structure described by Volborth † in *Glyptosphæra Leuchtenbergi* (Pl. I. fig. 15, *d*); and the 'Nature' reviewer adds:—"More closely still does it resemble the 'reniform groove' or 'semilunar pore' figured by Forbes in the fossils which he called *Apiocystis* and *Echinoëncrinus*." The same idea had also occurred to myself, and I have been led to conclude that there are a large number of Cystids in which an opening like that of the water-pore of recent Echinoderms is represented, and that it occupies a position close to the peristome in or near the interradius CD.

* *Op. cit.* p. 43.

† 'Ueber die russischen Sphaeroniten,' p. 29, pl. x. fig. 1.

The fourth opening of *Aristocystis* (*d*) is situated immediately behind the elongated peristome, generally towards its left end; though sometimes it is a little nearer the centre (Pl. I. figs. 12, 13). The position of the third or genital opening (*c*), however, seems to vary considerably in this type as depicted in Barrande's figures. It is sometimes on the very edge of the anal opening (*b*), as shown in fig. 12, while in other individuals it is nearly halfway towards the peristome (fig. 13), as in *Protocrinus oviformis*. The former condition obviously suggests that in other Cystids, in which no third opening has been discovered, the genital ducts and rectum may have opened together into the space beneath the valvular pyramid, through which they would have had a common outlet to the exterior, analogous to the "anal spiracle" of the Blastoids. Volborth *, de Verneuil †, and Roemer ‡ long ago suggested this as a possible explanation of the function of this structure, and we now know of a precisely similar case among certain Starfishes.

In the members of the family Pterasteridæ there is a sort of marsupial pouch on the dorsal surface of the disk, into which the oviducts and the anus both open, and it communicates with the exterior by an opening which Sladen has termed the oscular orifice. In the genera *Hymenaster* and *Pythonaster* this opening is guarded by five fan-like valves §, each composed of a number of spines united by perisome; but while in *Hymenaster* the marsupium or nidamental cavity covers the entire disk, owing to the great development of the supradorsal membrane, it seems to be reduced in *Pythonaster* to the small space within the oscular valves. Many Cystids were probably in this condition, *i. e.* with a valvular osculum common to the oviducts and rectum—*e. g.*, *Agelacrinus*, *Amygdalocystis*, *Comarocystis*, *Caryocrinus*, *Hemicosmites*, *Malocystis*; though it is of course possible that they may have had a separate genital opening which has not yet been discovered. In eleven of the twenty-one genera in which the third opening has been described, whether as the anus or as the genital pore, it is situated behind the mouth in the same interradius as

* Bull. Acad. Imp. Sci. St. Pétersbourg, 1842, tome x. p. 295.

† 'Géologie de la Russie d'Europe et des Montagnes de l'Oural,' par Murchison, de Verneuil, et Keyserling: Londres et Paris, 1845, vol. ii. p. 27.

‡ 'Lethæa Geognostica,' Bd. i. p. 263.

§ Zool. Chall. Exp., "Report on the Asteroidea," vol. xxx. 1889, p. 469, pl. lxxxiv. figs. 1, 3, pl. xcv. fig. 1.

the osculum, or nearly so *. This is well shown in *Aristocystis* (Pl. I. figs. 12, 13) and *Glyptosphæra* (fig. 15), both of which, and perhaps also *Pyrocystis* (figs. 10, 11), had a fourth opening (*d*) in the same interradius, which must, I think, be regarded as excretory in function.

The small second opening (*c*) in the anal interradius CD has been generally considered, of late years, as a genital pore; but the condition of *Aristocystis* shows the probability of its fusion with the anus (Pl. I. figs. 12, 13). Hence in *Echinoencrinus* and its six allies † (which have no second opening in the anal interradius) the oviducts and rectum may have had a common oscular opening, as supposed for *Agelacrinus* and *Caryocrinus*. But if so, what was the third opening, that in interradius DE, of these types? If genital, its position outside the anal interradius is somewhat anomalous; and I cannot help suspecting that it may be an excretory pore. The researches of the Sarasins seem to indicate that the problematical ovoid gland of *Asthenosoma* is really a kidney which opens externally through the madreporite ‡; and they point out that Prouho's description of the ovoid gland and its connections in *Dorocidaris* § is capable of a similar interpretation; though Cuénot's studies of the Asterids and Ophiurids have led him to regard this organ as essentially a lymphatic gland which produces the amœbocytes of the cœlom and vascular system ||. Kowalevsky ¶, on the other hand, concludes from his experiments that it is an excretory organ; and I am inclined to think that there is much to be said for this view of its function,

* *Aristocystis, Caryocystis, Deutocystis, Echinosphæra, Glyptosphæra, Megacystis, Orocystis, Proteocystis, Pyrocystis, Protocrinus, Sphæronis.* This third opening is possibly also present in *Allocystis*, Miller, and *Trochocystis*, Barrande, though its position is not easy to determine from the published figures of these types. That of *Eucystis* seems to be in interradius BC.

† *Apiocystis, Callocystis, Cystoblastus, Cryptocrinus, Echinoencrinus, Glyptocystis, Sphærocystis*, and possibly *Lepadocrinus*.

‡ "Ueber die Anatomie der Echinothuriden und die Phylogenie der Echinodermen," Ergebnisse Nat. Forsch. Ceylon, 1888, Bd. i. Heft 3, pp. 105–114.

§ "Recherches sur le *Dorocidaris papillata*, et quelques autres Échinides de la Méditerranée," Arch. de Zool. Exp. et Gén. 2e sér. vol. v. 1888, pp. 114–119 (of separate copy).

|| "Études anatomiques et morphologiques sur les Ophiures," *ibid.* vol. vi. 1888, pp. 50, 66. See postscript, *infrà*, p. 45.

¶ "Ein Beitrag zur Kenntnis der Excretionsorgane (Schluss)," Biol. Centralbl. 1889, Bd. ix. pp. 73, 74.

which does not necessarily exclude that advanced by Cuénot. So far as the Crinoids are concerned, it seems to me not unlikely that the structure at the ventral end of the ovoid gland, which I have described as the labial plexus *, or at any rate the specially modified portion of it which forms the spongy organ, may be nephridial in function. It is most largely developed round the hinder part of the peristome, between it and the anus; while the inner ends of some of the water-pores open in close proximity to it, and may even be in connection with it, as described by Perrier †.

Wachsmuth and Springer have recently suggested that the apparently poriferous plate between the mouth and anus of *Cyathocrinus* is a madreporite ‡, and their view is supported by the fact of this being the primary position of the water-pore in the larval Echinoderm.

Under these circumstances there is much reason to think that Volborth § was right in suggesting that the plicated triangular structure between the mouth and genital pore of *Glyptosphæra Leuchtenbergi* may be a madreporic plate. Quenstedt ‖ says that it seems to consist "aus drei welligen Klappen, ... und niemals fehlt." It is well shown in the two figures of the Russian species in Angelin's 'Iconographia'¶, and is explained by Lovén as the "rhombus"; but there is no indication of it in Zittel's figure of the same type **, nor is it mentioned in his generic description. Steinmann †† figures it, however, and compares it to a madreporite. Barrande ‡‡ compared it, and I think rightly so, to the slit-like opening just behind the peristome of *Aristocystis* (Pl. I. figs. 12, 13); while the 'Nature' reviewer extended the comparison to the opening at the edge of the peristome, just above plate 18, in the British *Echinoencrinus*, which Forbes had regarded as the anus §§. There would seem, however, to be something wrong about Forbes's description of this opening as being on the right

* 'Report upon the Crinoidea of the 'Challenger' Expedition,' 1885, p. 98.

† 'Mémoire sur l'Organisation et le Développement de la Comatule de la Méditerranée,' 3me Partie, Nouv. Arch. du Muséum, 3e série, t. ii. (Paris, 1890) p. 69.

‡ "The Perisomic Plates of the Crinoids," Proc. Acad. Nat. Sci. Philad. (1890 p. 358, pl. ix. fig. 7.

§ 'Ueber die russischen Sphaeroniten,' p. 29, Taf. x. fig. 1.

‖ 'Encriniden,' p. 694.

¶ *Op. cit.* tab. xi. figs. 1, 2.

** 'Paleontologie,' Bd. i. p. 416.

†† *Op. cit.* p. 178.

‡‡ *Op. cit.* p. 45.

§§ *Loc. cit.* p. 485, pl. xviii. fig. 3.

side, above plate 15; for his figures of *E. armatus* on pls. xviii. and xix. show that it is on the left side above plate 18, *i. e.* in interradius DE. He assigned a similar position to the anus or "reniform groove" of *Apiocystis pentremitoides*; but Hall * was "unable to observe the reniform groove or pore on the right side near the apex" of *A. elegans*, while he found one, or possibly two, on the left side above the plate which he marked 16, though I should call it 18, as I have already pointed out. Hall took these to be the mouth and anus. But what he called the "single straight groove in the direction of the back and front of the body" is now known to be the linear peristome containing the mouth; and should the second opening described by him really exist, we must, I think, regard it as excretory, while the other, if present, may be genital. The same remark applies to *Callocystis*, in which the peristomial plates of interradius DE are pierced, according to Hall †, by the mouth and anal pore, and also bear a little porous tubercle which "strongly reminds one of the madreporiform tubercle in *Asterias* and other Echinoderms."

Further information about these structures is much to be desired, and it is quite possible that the "porous tubercle" of *Callocystis* may be of the same doubtful nature as the similarly-named structure which Hall described a few pages further on in *Hemicystis*, though later writers have made no allusion to it. Another of Hall's genera, *Sphærocystis* ‡, has a small opening close to the peristome in the same interradius DE. It also occurs in *Glyptocystis multipora*, as described and figured by Billings §, while Lovén marked it as the genital aperture in Angelin's figure of the summit of *Cryptocrinus lævis* ‖.

I am inclined to think that in all these genera with no separate genital opening in interradius CD, which seems to be its normal position, there was a common osculum for the anus and genital ducts, as in *Hymenaster*; while the lateral opening in interradius DE was excretory in function. Indeed, one might almost say that it represented a madreporite, and also placed the water-vascular system in communication with the exterior. The presence of this aperture in the same position in seven of those genera which have a pentamerous and dicyclic dorsal cup like that

* 'Palæontology of New York,' vol. ii. p. 243, pl. li. figs. 7, 8.
† *Ibid.* pp. 238, 240.
‡ 'Palæontology of New York,' vol. iii. p. 130, pl. vii. A, figs. 1–5.
§ *Loc. cit.* p. 56, pl. iii. fig. 1 *g*. ‖ *Op. cit.* tab. xii. fig. 3.

of a Crinoid is a point of some interest, and may prove to be of use for purposes of classification. I would likewise assign an excretory function to Volborth's organ in *Glyptosphæra* and the fourth opening in *Aristocystis* (Pl. I. figs. 12, 13, 15), and it is quite possible that Volborth was correct in regarding the former as a madreporite. At any rate it occupies the same position, relatively to the genital pore, the mouth, and the anus, as the madreporic opening has in those Holothurians in which it retains its primitive connection with the exterior; and we must not lose sight of the possibility that there may have been Cystids which had a distinct external madreporic opening in early life, though it subsequently closed up, as is the case in many Holothurians.

Thus, for example, it may have remained permanently open in *Glyptosphæra* and have closed in *Protocrinus*, the nephridial duct, if such existed, perhaps acquiring a communication with the exterior through a genital pore. I do not wish to be understood as implying that I fully believe this to be the case. But in endeavouring to throw some light upon the morphology of these ancient forms, one must not lose sight of the possibilities of explanation afforded by their recent representatives.

The analogy of *Glyptosphæra* and *Aristocystis* would seem to indicate that when there is a distinct opening *between* the mouth and anus, as in *Sphæronis*, *Protocrinus*, and *Proteocystis*, it should be recognized as genital; though we might, of course, look upon it as excretory, and assume that there was a common oscular orifice for the anus and genital ducts, as I have done for *Agelacrinus* and *Caryocrinus*. I must confess that I am rather inclined to take this view of *Sphæronis* *, which has a large anal pyramid just behind the mouth, and a minute valvular opening close to the left posterior ambulacrum (D) which may very well have been excretory in function. It is quite possible also that the third opening of *Caryocystis*, *Echinosphæra*, and *Megacystis* was nephridial or madreporic, rather than genital †, though it might, of course, have served both functions, as suggested above. This possibility is to some extent supported by the embryological fact that the primary water-pore of Echinoderm larvæ is situated in the anal interradius, which also contains the chief part of the labial plexus and ovoid gland of a Crinoid,

* See Angelin's 'Iconographia,' tab. xi.

† See postscript, *infrà*, pp. 49, 50.

i. e. the supposed kidney. On similar grounds, too, we might regard the lateral pyramid of *Agelacrinus* as the common oscular orifice of the nephridial, genital, and digestive systems.

The above argument is based on the supposition that the Cystids had an ovoid gland (kidney, *Sarasin*) like the Crinoids and Urchins; but there is also the possibility that in some among them, *e. g.* the less Crinoid-like forms, such as *Caryocystis* and *Megacystis*, the excretory and amœbiform functions of the ovoid gland were performed by the so-called "water-lungs," as seems to be the case in the Holothurians with no external madreporite. These organs open into the cloaca, together with the rectum, of which they are primitively diverticula, and the cloacal opening (anus) is more or less protected by valvular plates which represent the pyramid of the Cystids. In either case, therefore, it seems probable that the lateral pyramid of *Agelacrinus*, *Cyathocystis*, *Caryocrinus*, and similar forms may have been both excretory and anal in function; while the analogy of *Hymenaster* and *Pythonaster* would suggest that it also served as the outlet of the genital products, so that these types with only one recognizable opening besides the mouth might be fairly described as Cystidean Monotremes.

3. Some General Considerations.

I have endeavoured to show in the early part of this paper that the dorsal cup of many Cystids is composed of plates which correspond respectively to the infrabasals, basals, and radials of a Crinoid. In former memoirs * I have likewise pointed out that these plates may be recognized in the larvæ of Asterids and Ophiurids, and also in many adults of both classes †. Dorsocentral basals, and perhaps radials, occur in the larval Echinid, and all persist in the adults of some generic types; though in others only the basals and radials are traceable, as in the Blastoids, which we may fairly assume to have had a dorsocentral at the base of the stem, just like the young Crinoid, and the same may be said of the stalked Cystideans. It is curious, however, that infrabasals, which are so frequently developed in the brachiate forms, should be unknown in the Urchins and also in the Blastoids, neither class possessing definite appendages in which the ambulacra terminate; and their absence in the Blastoids is the

* See more especially the chapter "On the Homologies of the Crinoidal Calyx in the other Echinoderms," Report on the Crinoidea, Zool. Chall. Exp. vol. xi. 1885, pp. 393–402.

† See postscript, *infrà*, p. 44.

more remarkable from the fact that they are so largely developed in the Cystids, in many of which, e. g. *Pseudocrinus* and *Callocystis*, the lateral appendages of the ambulacra seem to have been of the same nature as the so-called pinnules of the Blastoids, though less numerous and more highly developed. I have the very strongest conviction that the basal and radial plates, and probably also the dorsocentral, constitute a fundamental part of the organization of every Echinoderm, except, perhaps, the Holothurians. They have not as yet been identified in any members of this class; but I think it by no means improbable that they might be found to have the same relation to the right enterocœl in the larvæ of the heavily-plated Psolidæ, as they have in other Echinoderms.

It is now some years since the publication of Lovén's classical studies of the apical system of the Urchins *, and his comparison of it with that of a Crinoid. In the words of the cousins Sarasin † :—

"In dem ganzen so vor Durchbruch des Afters von elf Platten bedeckten Apicalpol sah nun Lovén die Hauptzüge einer Bauart, welche man bis dahin als dem Echinidentypus nicht zugehörig, sondern als characteristisch für den Crinoidentypus betrachtete, und er benutzte dies zu einem Versuche, die Echiniden von den Crinoiden abzuleiten."

The Sarasins speak of this appearance as the "Crinoidenfantom der Echiniden," referring to me as one of its "emsigsten Verfolger;" and they bring a variety of arguments against a Crinoid ancestry for the Urchins, while they endeavour themselves to prove that all the classes of Echinoderms are derived, directly or indirectly, from the Holothurians.

It seems to me, however, that the so-called "Crinoidenfantom" is one of the Sarasins' own making, and that they have completely misapprehended the position of Lovén and myself. They do not refer to a single passage in Lovén's writings which indicates that he regards the Crinoids as in any way the ancestors of the Echinids. He did say, however ‡ :—"Dans l'une et l'autre de ces grandes classes d'Échinodermes le système dorsocentral, se présentant sous des aspects divers, est donc identique dans ses traits principaux de conformation." Farther on in the same volume he pointed out that the dorsocentral system of a young Asterid is

* "Études sur les Échinoïdées," K. Svensk. Vetensk. Akad. Handl. 1874, Bd. xi No. 7, pp. 65–91.

† *Op. cit.* p. 142. ‡ *Loc. cit.* p. 72.

closely similar to that of the young Echinid, and on p. 89 he said:—

"Il existe, entre le système dorsocentral des Astériadées et celui des Échinoïdées, considéré dans sa totalité et dans ses rapports aux autres systèmes du test, comme dans ses parties constituantes, une similitude de structure et une conformité de modifications qui achèvent de faire concevoir tant l'unité de son plan morphologique primitif, que la nature identique du jeu des organes qui y apportent les altérations caractéristiques des unes et des autres."

I do not know of any passage in Lovén's writings which would authorize the Sarasins in saying that he attempted to derive the Echinids from the Crinoids. They are described in his work on *Pourtalesia* * as the "joint-heirs" of some remote ancestral type; and the Sarasins seem to have altogether forgotten or to be unacquainted with the following remarks on p. 57 of the same memoir:—

"And so close is in reality, on either side, the general conformity in structure of the geminous pores, as to cause the lineage of the Archæonomous Echinoidea to gravitate forcibly towards that group of antique Cystoidea of the Silurian era, different as these no doubt were in other respects, in the total absence—at least in the adult—of a calyx, and in the distribution of the pores all over the perisome."

Further on, in the same work (p. 61), Lovén described his own position as follows:—

"Years ago it occurred to me, as it had to others, that the general resemblance of the 'apical' system in the Cidaridæ, Saleniadæ, and Echinidæ to the calyx of certain Crinoidea, might be a morphological fact of importance with regard to a true perception of the homologies of the skeletal constituents in the Echinoderms generally."

And on the next page he says:—

"It was at a very remote geological period that the classes of the Echinoderms branched off from their ancestral trunk, at the same time inheriting in common certain important characteristics, the actual presence of which still holds together their diversified forms."

Although differing from Lovén as regards some of the particular plates which are mutually homologous in the apical systems of Crinoids and Urchins respectively, I hold as strongly as he does that the apical system is fundamentally identical in structure in all the Echinoderm classes in which it is represented. This has been my position ever since I began to write on the subject in 1878†.

* *Loc. cit.* p. 81.

† "On the Oral and Apical Systems of the Echinoderms," Quart. Journ. Micr. Sci. 1878, vol. xviii. p. 351.

I have designedly abstained from all speculations respecting the origin of the Echinoderms, though I have once or twice alluded to various facts which seem to show that the Crinoids are in a more embryonic condition, and consequently represent an earlier phylogenetic stage than the other classes. But this is a very different thing from regarding them as the ancestral forms of the Urchins, and I would ask the Messrs. Sarasin to quote any passage from my writings which shows that I have ever held this view.

If I understand them rightly, they altogether deny that any homology can be traced between the calyx-plates of a Crinoid and those forming the primary apical system of an unstalked Echinoderm *. They do not seem to consider the embryological evidence (which has been greatly strengthened since their memoir appeared by the researches of Fewkes † and Bury ‡) as deserving of any consideration at all, for they say on p. 147, "Das Auftreten von Kreisen aus je fünf oder zehn platten bei Echiniden und Crinoiden beruhrt auf secondärer Vereinigung ursprünglich ungeordneter kleinerer Plättchen, analog dem Verschmelzen von primären Ambulacralplatten zu Grossplatten;" while on p. 151 they become somewhat sarcastic about the variations in the arrangement of the apical plates of Ophiurids, and the difficulty of

* Stürtz has recently made an extraordinary blunder respecting the apical system of the Ophiurids (*loc. cit.* p. 241). Referring to Neumayr's remarks upon it, he asserts that the centrodorsal rosette of these forms represents "das Mundskelet in der dorsalen Ansicht," and he thinks that on this subject "dürfte jetzt wohl kein Zweifel mehr bestehen." Stürtz is here confusing what Boehm called "die fünfteilige Rosette" in thinly-plated disks with the rosette of primary plates in the more heavily-plated forms. The former appearance is, no doubt, due to shrinkage and to the prominence of the mouth-skeleton beneath; but if Stürtz will look at the figures of the dorsocentral systems of *Ophiomusium* and *Ophioglypha* in the early plates of Lyman's 'Challenger' Report, he will discover his mistake. The dictum that the very substantial rosette of such forms or that of *Ophiopyrgus Wyville-thomsoni* (pl. ix. figs. 16, 17) is a dorsal view of the mouth-skeleton, can only be due to an inadequate knowledge of the subject. His error is the more curious as he refers to the "Rückenappendix" of *Ophiopyrgus* on p. 244.

† "On the Development of the Calcareous Plates of *Amphiura*," Bull. Mus. Comp. Zoöl. 1887, vol. xiii. pp. 120–131; and "On the Development of the Calcareous Plates of *Asterias*," *ibid.* 1888, vol. xvii. pp. 4–45.

‡ "The Early Stages in the Development of *Antedon rosacea*," Phil. Trans. 1888, B, pp. 269–293; and "Studies in the Embryology of the Echinoderms," Quart. Journ. Micr. Sci. 1889, vol. xxix. pp. 432–445.

comparing them with those of Crinoids. Perhaps they would have been less so had they been acquainted with the structure of the genus *Acrocrinus*, in which the radials are separated from the basals by three or four rings of plates, and may also be separated laterally as well. Variations from the primitive arrangement of the same kind, though scarcely greater in degree, occur among the Ophiurids; but I do not see that this in any way affects the homologies of the basal and radial plates in the Ophiurids and Crinoids respectively.

I am glad to find, however, that the Sarasins admit the complete correspondence between the oral system of *Psolus* and that of *Hyocrinus*. But they do not seem to be aware that this was described by myself twelve years ago *, when I also pointed out that oral plates corresponding to those of the Neocrinoids are developed in two Holothurian larvæ, besides persisting in the adult Psolidæ. We have seen that they are present in many Cystids, and they are also present in some Blastoids (*Elæacrinus*). Götte † and Bury ‡ have pointed out that they are the actinal representatives of the basals in the Pentacrinoid larva; and as Wachsmuth § took the same view of the so-called proximals in the summit of the Palæocrinoids, I was led to regard these also as orals ||, an opinion which, as we have already seen, the American authors have at last adopted ¶. I have pointed out above how this doctrine is strengthened by the correspondence between basals and orals in the non-pentamerous forms, such as *Caryocrinus* and *Rhizocrinus*, a fact which I commend to the notice of the Sarasins. The mouth-plates of Ophiurids are now generally recognized as orals, and there are strong reasons for regarding the so-called odontophores of Asterids as belonging to the same category **. Their presence in the Urchins is doubtful, except,

* "On the Apical and Oral Systems of the Echinodermata, Part II.," Quart. Journ. Micr. Sci. 1879, vol. xix. p. 191.

† "Vergleichende Entwickelungsgeschichte der Comatula Mediterranea," Archiv f. mikr. Anat. 1876, Bd. xii. p. 621.

‡ Phil. Trans. 1888, B, p. 270.

§ "Notes on the Internal and External Structure of Palæozoic Crinoids," Amer. Journ. Sci. 1877, vol. xiv. p. 189.

‖ Quart. Journ. Micr. Sci. 1879, vol. xix. p. 182.

¶ Proc Acad. Nat. Sci. Philad. 1888, p. 348. As already noted, this statement refers to the four anterior proximals only.

** See Sladen, "On the Homologies of the Primary Larval Plates in the Test of Brachiate Echinoderms," Quart. Journ. Micr. Sci. 1884, vol. xxiv. p. 40. See also the postscript to this paper, *infrà*, pp. 43, 44.

perhaps, in *Leskia mirabilis*. But so far as the other groups are concerned there can now be little doubt that the presence of five primary plates developed interradially on the left larval antimer is a fundamental morphological character. Bury * has recently shown that the terminal plates of the Stellerid arms are the radial plates of the left antimer, corresponding to the radials of the abactinal system. They may, or may not, be present in other groups, a point which I hope to discuss at some future time. But I am most strongly of opinion that the plates forming the apical and oral systems of Echinoderms cannot be left out of consideration in any discussion respecting the phylogeny of the group; and if Semon † would modify his Pentactula theory to the extent of admitting that his ancestral larval form (*Pentactæa*) had both abactinal and actinal radial and interradial plates, I should be greatly inclined to accept his general conclusions. He assumes, however, that the ancestral Echinoderm had "kein festes Skelett," and on p. 108 states his opinion that no true homologies are traceable in the apical system, "sondern nur sehr täuschende Analogieen." His acquaintance with the literature of the subject does not seem to be very extensive, for he states in a later paper ‡ how "zwei eifrige Anhänger Carpenter's wie Sladen und Bury die Terminalia der Asteroiden und Ocellarplatten der Echiniden für nicht homolog den ersten Radialia der Crinoideen halten." Semon appears to be altogether unaware that as long ago as 1884 I accepted Sladen's suggestion that the homologues of the radials of a Crinoid are to be found, not in the terminals of Asterids, but in the radial plates of the apical system §. If Semon will refer to the two papers of that date by Sladen and myself ||, or to the chapter on this subject in the "Report on the

* Quart. Journ. Micr. Sci. 1889, vol. xxix. pp. 432-442.

† "Die Entwickelung der *Synapta digitata*, und die Stammesgeschichte der Echinodermen," Jenaische Zeitsch. Naturwiss. 1888, xxii. Bd. N. F. xv. p. 78 (of separate copy).

‡ 'Die Homologien innerhalb des Echinodermenstammes," Morphol. Jahrb. 1889, Bd. xv. p. 299.

§ On this subject Neumayr remarked (p. 500):—"Auch bei *Zoroaster fulgens* (Quart. Journ. Micr. Sci. vol. xxiv. Taf. 1. fig. 16) ist die von Sladen als 'Radiale' bezeichnete Platte nur das grösste proximale Glied der homologen Reihe dorsaler Armtafeln." It is curious that Neumayr should not have remembered that the same description applies to the radial plates of a Crinoid.

|| Quart. Journ. Micr. Sci. 1884, vol. xxiv. pp 3, 32.

'Challenger' Crinoids *, he will find that our views are identical, and not divergent as he states. I freely admit that Bury thinks it probable that the oculars of an Urchin are terminals and that the primary radials are unrepresented †. But the occasional entrance of the oculars into the basal ring, and the resemblance of *Tiarechinus* to a Blastoid ‡, are small difficulties in the way of accepting this view without the strong proofs which will, I hope, soon be forthcoming. It may be that the primary abactinal radials are not developed in the Urchins any more than the infrabasals are. But if the plates hitherto regarded as such should really prove to belong to the left antimer, another piece of evidence will be afforded in favour of the view that the ancestral Echinoderm had radial as well as interradial plates developed on the actinal hemisome, in relation with its left body-cavity.

It may be noted, too, that Bury's observations on Echinoderm larvæ answer many of the objections brought forward by the late Professor Neumayr against the views of those who believe the apical system of all Echinoderms to be constructed upon a common plan, modified though it be to a very considerable extent among the different members of the group. Neumayr attacked the subject with very great skill, but almost entirely from the palæontological side; and I do not think that he gave due consideration to the evidence either of embryology or of comparative anatomy.

To discuss his arguments in detail would be impossible now; but I hope to do so at some future time, when I shall also propose to consider the varying theories of Semon and the Sarasins, of Stürtz and Walther respecting the phylogeny and mutual relationships of the different Echinoderm classes. One point, however, and that a fundamental one, I cannot pass without notice.

Neumayr stated § that "von der richtigen Deutung des Seeigelscheitels hängt zum grossen Theile das richtige Verständniss der ganzen Entwicklung der Echinodermen ab, und ganz speciell ist hiebei das Verhältniss der Genital- und Ocellartäfelchen zueinander von grösster Bedeutung." Taking as a starting-

* *Op. cit.* pp. 393–402.

† Quart. Journ. Micr. Sci. 1889, vol. xxix. p. 442. Bury's view has been adopted quite recently by Janet and Cuénot ("Note sur les Orifices Génitaux multiples," &c., Bull. Soc. Géol. France, tome xix. p. 303.

‡ If it be a valid argument that the oculars of an Urchin are terminals and not radials, because of their relation to the ambulacra, it is equally applicable to the radial plates of a Blastoid, which are universally accepted as homologous with those of a Crinoid.

§ *Op. cit.* p. 363.

point the Ordovician *Bothriocidaris Pahleni*, which has a single ring of ten plates enclosing the anal system, he identified five of these as the genitals and five as the oculars. He then continued:—

"Wir können daraus mit Sicherheit schliessen dass bei den uralten Grundformen der Seeigel die Theile aus welchen sich die Genital- und Augentäfelchen der späteren Typen entwickelt haben, nicht schon zu zwei fünfzähligen, sondern zu einem einzigen, aus gleichwerthigen Stücken bestehenden zehnhzähligen Kranze angeordnet waren. Damit ist die wichtigste Frage in der ganzen Morphologie der fossilen Seeigel gelöst, oder die richtige Deutung ergibt sich wenigstens von diesem Standpunkte aus ziemlich einfach von selbst, und wir werden sehen dass dieses Ergebniss für das Verständniss des ganzen Stammes der Echinodermen von grundlegender Bedeutung ist." (P. 364)

Neumayr made use of these statements later on in the book (p. 368) as an argument against the identification of the ocular and genital plates of an Urchin with the radial and interradial plates developed in two rings round the apical pole in other Echinoderms, saying that the condition of *Bothriocidaris* shows the impossibility of the dicyclic arrangement being the primary one.

Neumayr's position thus depends on two fundamental assumptions:—

1. Genital and ocular plates are present in *Bothriocidaris Pahleni* and are arranged in a single ring, not in two concentric rings, as in later forms.
2. Because *Bothriocidaris Pahleni* is the oldest known Urchin, therefore we are entitled to regard the structure of its apical system as the primitive one for Urchins, and to extend this view to the other Echinoderms.

But was Neumayr right in asserting the presence of genital and ocular plates in *B. Pahleni*? Schmidt *, in describing the genus, said expressly "Von Genital- und Ocellarplatten keine Spur;" and neither Lovén, Agassiz, nor Zittel make any reference to their presence in this type, though Duncan † adopted Neumayr's views. It may be that the five large plates at the ends of the ambulacra are the oculars. But is it so certain that the smaller plates alternating with them are the genitals? Neumayr took this for granted, though none of his predecessors had ever suggested it, and he did not offer a single argument in support of his opinion. Schmidt considered them as the uppermost plates

* Mém. Acad. Imp. Sci. St. Pétersb. 1874, tome xxi. No. 11, p. 38.

† "A Revision of the Genera and Great Groups of the Echinoidea," Journ. Linn. Soc., Zool. 1889, vol. xxiii. p. 8.

of the interambulacra *, and the characters of these plates in *Bothriocidaris Pahleni* and *B. globulus* respectively seem to me to afford strong evidence that he is right. In *B. Pahleni* the plates of the interambulacral zones are without tubercles, and so are the supposed genital plates; but in *B. globulus* there are tubercles on the interambulacral plates and also on the so-called genitals. Neumayr made no reference whatever to Schmidt's figure of the latter species, which shows eleven plates, not ten, in the periproctal ring, while there are two others which almost enter it. Schmidt † describes the apex in the following terms:—

"Die Scheitelgegend ist complicirter gebildet, weil die Interradien in kleinen unregelmässigen länglichen Täfelchen bis zur Afteröffnung fortsetzen, und die fünf Scheiteltafeln, die auch hier auf je Einem Paar der letzten Ambulacraltafeln aufsitzen, den Kreis nicht schliessen."

Another difficulty in the identification of these terminal interambulacral plates with the genitals of later Urchins is that they occupy a more distal position in the periproctal ring than the radially placed or supposed ocular plates do. In fact, in *B. Pahleni* one of them is excluded from the border of the periproctal ring altogether, as the edges of the radials meet inside it. Neumayr was fully aware of this ‡; but it does not seem to have made him in any way doubt the correctness of his identification of these plates as genitals:—

"Wir sehen also, dass hier ein Verhältniss herrscht, welches demjenigen bei jüngeren Seeigeln gerade entgegengesetzt ist. Bei der Annahme zweier fünfzählige Kränze würden hier die Augentäfelchen den inneren, die Genitaltäfelchen den äusseren derselben bilden. Eine solche Umkehrung ist eine absolut Unmöglichkeit."

With the last remark I am quite in accordance. But considering that there are other strong reasons against Neumayr's novel interpretation of these plates as the genitals, I cannot agree with him in attaching so much importance to the condition of *Bothriocidaris* as to make it altogether outweigh the evidence afforded by the comparative anatomy and embryology of the Echinoderms generally. Even if it be granted that Neumayr's

* *Loc. cit.* pp. 39, 41.
† *Loc. cit.* p. 41, Taf. iv. fig. 2 *b*.
‡ *Op cit.* p. 364.

view of these ten plates is the correct one, that is no proof that they did not develop in two rows in *Bothriocidaris* as in other Echinoderms. There are many of the later Urchins in which some or all of the oculars come into the border of the periproct and form a closed ring with the basals or genitals; and they occupy a similar position in certain Ophiurids. But all our knowledge of the comparative anatomy and embryology of these two classes goes to show that this condition is not the primitive one. Why should it be assumed, therefore, that this was necessarily the case in the antique *Bothriocidaris*? Are all the conclusions of morphology and embryology respecting the fundamental structure of a great subkingdom to be set aside in favour of those deduced from the adult characters of the earliest known fossil member of one of its classes, though by no means the most ancient representative of the subkingdom? If this be the case, the palæontologist will become the absolute arbitrator in all phylogenetic discussions; and the results of years of thought and study must at once be set aside if they are not compatible with the characters of a particular fossil, which is liable at any moment to be displaced from its position as the earliest known, and therefore the most primitive type of any group.

It seems to me that the palæontologist is here assuming too much; and as regards this particular case, a curious fact has recently been noted which goes a long way to prove the untenability of Neumayr's position. Duncan * has pointed out that in some individuals of *Palæechinus sphæricus* the radial plates are intercalated between the genitals (basals) and form with them a ring round the periproct. But, on the other hand, there are other individuals of the same species in which "the five radial plates are triangular and are only intercalated between the basal plates on the outside of the system, and they do not form a part of the ring or margin of the periproct." There is a third condition in which the radial plates are altogether absent, and the basals form a closed ring. This was represented by de Koninck †, whose figure was reproduced by Neumayr, and he proposed to make the

* "On some Points in the Anatomy of the Species of *Palæechinus* (Scouler), McCoy, and a proposed Classification," Ann. & Mag. Nat. Hist. ser. 6, vol. iii. 1889, p. 196.

† "Sur quelques échinodermes remarquables des terrains paléozoïques," Bull. Acad. Sci. Bruxelles, 1869, 2e série, tome xxviii. p. 545, fig. 1.

original the type of a new genus *Typhlechinus* *. Duncan's observations seem to render this unnecessary, and he was inclined to attribute the apparent absence of radial plates in de Koninck's specimen "to crush and irregular pressure, so that the radial plates were either pushed into the test or pressed away." Further investigations upon this point are much needed.

If *Palæechinus sphæricus* were the oldest known Urchin, which of these conditions would Neumayr have recognized as the typical one, and as representing the primitive structure of the apical system, not only in the Urchins, but also in the Echinoderms generally? These considerations seem to me to tell very strongly against his doctrine that this primitive type is to be found in *Bothriocidaris*, even if we assume, which I do not, that genital plates are represented in this type. If they existed, they were at any rate imperforate, and it would seem, therefore, as if the so-called anal opening may really have been a valvular osculum common to the rectum and genital ducts, like that of the *Pterasteridæ* and certain Cystids.

It is to be noted, too, that there is no distinct indication of the presence of a madreporite in this genus. It is true that Schmidt describes "ein System von länglichen Furchen und Rippen" on one of the five large plates at the apex of *B. globulus* which he identifies as the madreporite †. But he does not seem to have noticed the anomaly of its position at the end of an ambulacral zone; and the plate which he thinks is of the same character in *B. Pahleni* is similarly situated. Zittel, while mentioning the presence of a madreporite, says nothing about its radial position; while Neumayr and Duncan made no reference to it in any way. It is not clear, therefore, whether Neumayr believed it to be absent in *Bothriocidaris* or situated in an ocular plate; but in either case the application of the same principle that he employed in arriving at the primitive type of the Echinoderm apical system would lead to somewhat anomalous results. If *Bothriocidaris*, in virtue of its geological position, is to be regarded as primitive in one structural feature, we must take the same view of its other morphological characters; and the conclusion is then forced upon

* *Op. cit.* p. 362, fig. 82 *c*. Neumayr described this figure somewhat inaccurately as "*Typhlechinus sphæricus* aus dem irischen Kohlenkalke. Nach Baily." But de Koninck gave the locality as Kirkby-Stephen in Westmoreland.

† *Loc. cit.* p. 41.

us, either that the primitive Echinoderm had no madreporite at all, or that it was situated in a radial plane, so that its interradial position in later forms must be "ein Stück stark gefälschter Entwicklungsgeschichte." Even if we suppose that a madreporic canal was present but opened through the osculum, as the oviducts must have done, the facts of embryology altogether preclude the possibility of our regarding this as in any way a primitive or ancestral condition; and I believe the same to be the case with Neumayr's doctrine respecting the primitive nature of the apical system in *Bothriocidaris*.

Postscript (September 1891).

1. *The Dorsocentral System.*

It has been pointed out above (pp. 33–39) that the views of Sladen and myself respecting the fundamental identity of the abactinal or dorsocentral system throughout the calyculate Echinoderms have not been favourably received by MM. Neumayr, Semon, and Sarasin. I am glad to say, however, that Professor Perrier, who formerly contested our position, has recently adopted it.

We were led, on various grounds, to doubt the correctness of his assertion that the primary interradial plates in the abactinal system of the young *Asterias* and *Brisinga* become the odontophores of the adult. In consequence of our criticisms, he reinvestigated the question in 1885, and still maintained that his former statements were correct*. Even as late as 1888 he wrote :—

"Les cinq pièces interradiales deviennent, sans contestation possible, les *odontophores* chez les *Brisingidæ*. Les figures de Lovén, mes observations sur de jeunes *Asterias spirabilis* ne me permettent guère de douter qu'il en soit ainsi chez certains *Asteriadæ*, quoique M. Fewkes m'ait affirmé que l'odontophore se forme d'une manière indépendante chez l'*A. berylina*" †.

Further investigation of larval Asterids, however, and also Fewkes's published observations ‡, have quite recently led Perrier

* "Première Note préliminaire sur les Échinodermes recueillis durant les campagnes de dragages sous-marins du 'Travailleur' et du 'Talisman.' I. Stellérides." Ann. Sci. Nat. 6me Série, Zool. tome xix. 1885, Article No. 8, p. 45.

† "Notions actuellement acquises sur l'organisation des Échinodermes," Biblioth. École d. hautes Études, Sci. Nat. tome xxxiv. 1888, Article No. 4, p. 81.

‡ Bull. Mus. Comp. Zoöl. 1888, vol. xvii. pp. 40–42.

to abandon this position*; and he now admits that "les odontophores des *Asterias* ne font donc pas partie du calice primitif; tout au plus pourrait-on les comparer aux plaques orales des Crinoïdes," as is done by Sladen and myself.

We have likewise ventured to question the interpretation put by Perrier upon the dorsal epiproctal appendage of *Caulaster* and the Astropectinidæ, which he regarded as homologous with the stem of a Crinoid. He has also given up this view and has adopted the current one, that the crinoid stem is a modification of the preoral lobe of the larval Echinoderm†. Further on in this same memoir Perrier seems to adopt, though with some reserve, Sladen's theory that the primary radial plates of Asterids remain upon the disk, and are not carried out as the terminals to the ends of the growing arms, as was formerly supposed. But in a still later publication he comes over altogether to our side‡. For he describes the calycinal system of *Calycaster* (n. g.) as consisting of dorsocentral, basals, and radials; while *Prognaster* (n. g.) has infrabasals as well; and he adds, "Le squelette du disque est, en effet, exactement constitué dans ces deux genres comme le squelette typique d'un Crinoïde, et c'est pourquoi nous appellerons *calicinales* les pièces fondamentales qui le constituent."

It is with much gratification that we have watched the gradual conversion of our distinguished French colleague to our views, as the result of his own investigations of various Starfishes, both larval and adult. I still entertain hopes that both Semon and the Sarasins will adopt them whenever they can find the time for detailed comparisons of the calycinal systems in various larval Echinoderms, and also, but especially Semon, for a more extensive study of the literature of the subject. In fact, all the German authors who have recently dealt with this question (Hoernes, Neumayr, the Sarasins, Semon, Steinmann, Stürtz, and Walther) seem to be more or less imperfectly acquainted with it; and much has therefore been published which would never have been

* 'Mission Scientifique du Cap Horn, 1882–1883,' tome vi. Zoologie. Échinodermes. I. Stellérides. Paris, 1891, p. 27.

† *Ibid.* p. 25.

‡ "Sur les Stellérides recueillis dans le Golfe de Gascogne, aux Açores et à Terre-Neuve, pendant les campagnes scientifiques du yacht 'l'Hirondelle,'" Comptes Rendus Acad. Sci. Paris, 1891, tome cxii. pp. 1225–1228.

written had the author got up his subject better; and yet the literature, while by no means extensive, is easily accessible.

The worst offender, however, in this respect is Neviani, who seems to be altogether unacquainted with any of the results arrived at by the reporters on the Echinoderms of the 'Challenger' and 'Blake' expeditions, and also with the palæontological work of Messrs. Wachsmuth and Springer. *Hyponome Sarsii*, the supposed recent Cystidean from Cape York, was shown in 1879 to be merely the detached disk of an *Antedon* *; and it was with some surprise that I found it mentioned by Neviani in his recently published article on the Phylogeny of Echinoderms †, which is so much behind the times that no further reference need be made to it.

2. *The Water-vascular System and its Relations.*

In a preliminary note to his forthcoming Morphological Studies on Echinoderms, Cuénot makes no reference to his former view of the "ovoid gland" as a factory of amœbocytes; but regards it as an organ of respiration and excretion, functions which may be shared by the water-vascular system, with which it is always more or less intimately associated ‡. Perrier, however, continues to maintain its plastidogenic functions :—

"Chez les Stellérides, Ophiurides, et Échinides, l'appareil ambulacraire est accompagné par l'*appareil plastidogène*, qui en reproduit toutes les dispositions essentielles. Cet appareil comprend un *corps plastidogène*, qui accompagne la tube hydrophore; un *anneau plastidogène* ou *anneau de Tiedemann*, presque contigu à l'anneau ambulacraire; cinq faisceaux de *tubes plastidogènes* ou *tubes de Ludwig*, qui suivent le trajet des tubes ambulacraires"§.

These "tubes plastidogènes" have been often described as blood-vessels, though Perrier refused to accord them this rank. I am glad to learn, however, that he admits their existence, which has been frequently denied. Like Durham, I prefer to distinguish the radial portions of the plastidogenic apparatus as the

* "Preliminary Report upon the Comatulæ of the 'Challenger' Expedition." Proc. Roy. Soc. 1879, vol. xxviii. p. 388; and also Quart. Journ. Micr. Sci. vol. xix. 1879, pp. 14, 30.

† "Appunti sulla fillogenesi degli Echinodermi," Rivista Italiana di Scienze Naturali, Ann. xi. 1891, fasc. 2, p. 6 of separate copy.

‡ "Études morphologiques sur les Échinodermes. Note préliminaire." Arch Zool. Exp. et Gén. 2me série, tome xix. 1891, p. xiii.

§ Biblioth. École d. hautes Études, Sci. Nat. tome xxxiv. 1888, Article No. 4, p. 71.

hæmal system, and to regard the remainder as mainly excretory in character, partly, of course, through its plastidogenic functions. Its relations to the ambulacral system are important in this respect, and have been well expressed by Perrier*:—

"L'appareil plastidogène est, en grande partie, un centre formateur d'éléments anatomiques; il est à remarquer que, d'une part, il contracte des rapports intimes de contiguïté avec l'appareil ambulacraire qui communique, en général, avec l'extérieur, et que, d'autre part, il peut recevoir directement de l'appareil absorbant, quand il existe, des matières assimilables."

It is almost needless to remark that the communication with the exterior is effected by the water-pores; and in this relation some recent observations of Field's † are especially interesting. For he has discovered the presence in *Bipinnaria* of "a stage with bilaterally symmetrical water-pores, homologous in their mode of origin, and probably in function, with nephridia."

I have a strong conviction that further researches on *Balanoglossus* and *Cephalodiscus*, to say nothing of the *Tunicates* and *Amphioxus*, will throw considerable light on the comparative morphology of these intimately associated ambulacral and plastidogenic systems of Echinoderms; while the relations of the latter to the genital organs, on which Perrier lays so much stress, afford an additional reason for thinking that the osculum of the monotrematous Cystids performed a triple function, as suggested above on pp. 27–32. Beddard's discovery of anal nephridia in *Acanthodrilus multiporus* is very suggestive in this connection; and he has also shown reasons for thinking that in this type "the genital funnels and a portion at least of the ducts are formed out of nephridia" ‡. He further points out that at one stage of development of this worm the nephridium branches and becomes segregated "into several almost detached tracts, communicating with the exterior by their own ducts." These are strongly suggestive of the multiple water-pores of an Echinoderm; while in a new Eudrilid recently studied by Beddard§ "the nephridial

* *Ibid.* p. 73.

† "Contributions to the Embryology of *Asterias vulgaris*," Johns Hopkins Univ. Circ. vol. x. 1891, No. 88, pp. 101–103.

‡ "On the Homology between Genital Ducts and Nephridia in the Oligochæta," Proc. Roy. Soc. 1890, vol. xlviii. p. 455.

§ "Preliminary Notice of a New Form of Excretory Organs in an Oligochætous Annelid," Proc. Roy. Soc. 1891, vol. xlix. p. 310.

system of the genital segments consists almost entirely of a complex system of tubes, which ramify in the thickness of the body-wall, which open by numerous pores on to the exterior, and are connected by a few short tubes with the body-cavity." With a little modification this description would be fairly applicable to the water-vascular system of an Echinoderm; and Field's observations show that there is much to be said for Hartog's conclusion *, that "the madreporic system of Echinodermata is morphologically and ontogenetically a (left) nephridium."

3. *The Oscular Orifice.*

Before I had finished correcting the proofs of the preceding pages I received, through the kindness of Mr. R. A. Blair, of Sedalia, Missouri, an advance copy of the Palæontology from the Seventeenth Report of the Geological Survey of Indiana. It is from the pen of that ardent species-maker Mr. S. A. Miller, who adds fifteen more to the nineteen species of *Holocystis* which he has already described from the Niagara group of Indiana, while Hall, the founder of the genus, described another half-dozen from Wisconsin. Like the reviewer of Barrande's "Cystids" in 'Nature,' I would emphatically protest against the continued use of the termination *ites* for most generic names of Cystidea. No modern palæontologist, not even S. A. Miller, who is an ultra-conservative in all matters of nomenclature, now writes *Cyathocrinites*, *Poteriocrinites*, or *Rhodocrinites*, as did their famous author, J. S. Miller, in 1821. Why, then, do our palæontological works contain such lengthy names as *Amygdalocystites*, *Anomalocystites*, and *Strobilocystites*? The editors of Angelin's 'Iconographia' wrote *Caryocystis*, *Eucystis*, *Glyptocystis*, *Gomphocystis*, and *Megacystis* in 1878, with the remark, "Nominum genericorum exitus in *ites*, regno lapideo principio proprius, regno animali alienus;" but their example has not been followed to any great extent. The change involves a feminine termination to the specific names, and also renders a new generic name necessary, for the name *Holocystis* was given by Lonsdale in 1849 to a well-known Cretaceous coral, and *Holocystites*, Hall, only dates from 1864. Hall himself drew attention to this fact somewhat later†

* "The True Nature of the 'Madreporic System' of Echinodermata, with Remarks on Nephridia," Ann. Mag. Nat. Hist. ser. 5, vol. xx. 1887, p. 325.

† "Twentieth Annual Report, New York State Cab. Nat. Hist.," Albany, 1867, p. 380.

with the following remark:—"The difference of the terminal syllable has in many cases been regarded as a sufficient distinction, and is perhaps preferable to adopting a new name. Should it be objected to, however, I propose the name *Megacystites*." This name, minus the terminal syllable, was adopted by the editors of Angelin's 'Iconographia,' who gave its synonymy in 1878 and described a new species from Sweden *. Miller quotes this work, but seems to be altogether unacquainted with the change proposed by Hall. For *Megacystis* does not appear in his 'North-American Geology and Palæontology,' nor in his recent contribution to the Seventeenth Indiana Report.

Another change seems also to be inevitable. *Echinodiscus* is one of the oldest generic names among the Sea-urchins, having been founded by Breyn in 1732. Descriptions of the genus and of three of its species appear on pp. 531–534 of the 'Revision of the Echinoidea' by Alexander Agassiz. In spite of this, however, and of Scudder's 'Nomenclator Zoologicus,' Messrs. Worthen and Miller bestowed the name *Echinodiscus* in 1883 on what they believed to be a new genus of Cystids allied to *Agelacrinus* †. They state that "the mouth or ovarian pyramid is subcentral, while in *Agelacrinus* it is submarginal. This elevation would seem to be homologous with the mouth in the Echinoids, for below it, within the visceral cavity, there occur several pieces which were evidently connected with the digestive functions, and therefore homologous with the jaws in the latter order." Six years later Miller described this same opening in *Agelacrinus* as the ovarian or anal aperture ‡, while he spoke of that of *Echinodiscus* simply as the "mouth;" and in his latest publication § he describes a new species, *E. Sampsoni*, in which "the mouth is distant more than half an inch from the central point of the union of the ambulacra." Nothing could better illustrate his extraordinary confusion upon this subject and his persistent disregard of the simplest facts in Echinoderm morphology.

It has been pointed out above that *Megacystis* is one of the genera which has a third opening situated behind the mouth in the same interradius as the osculum. Miller continues to call

* *Op. cit.* p. 29.

† 'Geological Survey of Illinois,' vol. vii. 1883, p. 335.

‡ 'North-American Geology and Palæontology,' p. 222.

§ 'Seventeenth Report of the Geological Survey of the State of Indiana,' Palæontology, p. 76.

the latter the mouth; while the real mouth (or rather its peristome) is the "ambulacral opening," whatever that may mean, and the third opening is supposed to be anal. I am inclined to regard this last as nephridial in function rather than genital, and as equivalent to the fourth opening of *Aristocystis* and *Glyptosphæra*. My reasons are as follows:—Miller describes and figures two examples of *Megacystis commoda* *, with the remark that it has two supposed anal openings, "one in the central part of each plate between the mouth and ambulacral opening." These two specimens show the same curious variation as Barrande's examples of *Aristocystis Bohemica* which I have figured on Pl. I. figs. 10, 11. In one of them the distal opening, which I regard as genital, is on the very edge of the anal aperture, while in the other it is nearly halfway up towards the peristome, separated from it, however, by the proximal (excretory) opening. Here, again, therefore, it seems to be a fair assumption that in the ordinary forms of *Megacystis*, as also in other ditrematous Cystids, there was a common outlet for the rectum and genital ducts, while the opening nearer the peristome was an excretory one. It would seem, furthermore, that in some species of *Megacystis* † this also became absorbed into the osculum. For, while it is immediately behind the peristome in *M. Gorbyi* and *M. scitula*, it is about halfway between the peristome and the osculum in *M. bacula*, *M. cannea*, and *M. Faberi*; while in four other species, *M. Hammelli*, *M. ornata*, *M. parvula*, and *M. rotunda*, it is nearer the osculum, sometimes indeed on its very edge, as shown in Miller's figures of the two first-named. Furthermore, in the case of three species ‡ Miller expressly mentions the absence of the third opening which he calls the anal aperture; while he gives good figures of the summit in well-preserved examples of five more § in which no third opening is visible in the single plate between mouth and osculum, though its absence is not mentioned in his descriptions. There is also no reference to it in some of his other descriptions, as also in those given by Hall, whose specimens, however, were only casts.

* *Ibid.* p. 14, pl. iii. figs. 2, 6.

† Miller's descriptions of his earlier species of *Megacystis*, or, as he calls it, *Holocystites*, will be found in vols. i. and ii. of the 'Journal of the Cincinnati Society of Natural History' (October 1878 and July 1879), and also in his 'North-American Geology and Palæontology.'

‡ *M. elegans*, *M. globosa*, *M. perlonga*.

§ *M. ornatissima*, *M. papulosa*, *M. parva*, *M. subovata*, *M. Wykoffi*.

We thus meet with the following conditions in the one genus *Megacystis*:—1. A common oscular opening for the rectum, genital and excretory ducts, as in *Agelacrinus*, *Amygdalocystis*, *Caryocrinus*, *Hemicosmites*, and *Malocystis*, (*M. elegans*). 2. A separate excretory opening near the peristome and an osculum for the rectum and genital ducts, as in *Caryocystis*, *Cystoblastus*, *Cryptocrinus*, *Glyptocystis*, *Orocystis*, *Sphæronis*, and *Sphærocystis*, (*M. Gorbyi*). 3. The excretory and genital openings independent of the osculum, as in *Aristocystis* and *Glyptosphæra*, (*M. commoda*). A fourth condition is possible, as I have suggested above, on p. 31. Where there is a single opening between osculum and peristome, but some little way from the latter (*M. bacula*), it may, perhaps, be both excretory and genital. I am inclined to think, however, that the balance of argument is in favour of considering the osculum as common to the rectum and genital ducts, like the anal spiracle of the Blastoids, unless a fourth opening is present. The third opening may therefore be generally regarded as excretory or nephridial in function, being situated sometimes in interradius CD (*Proteocystis*, *Protocrinus*, and *Sphæronis*), sometimes in DE (*Cryptocrinus*, *Cystoblastus*, and *Glyptocystis*), and sometimes in BC, as in *Eucystis* and possibly also in some forms of *Caryocystis* and *Echinosphæra*.

Several of Miller's latest figures of the summit of *Megacystis*, especially those of *M. commoda*, *M. Gorbyi*, and *M. scitula* *, in which the peristome was more or less oblong in shape, seem to me to indicate that it was covered by a low pyramid of oral plates, which have fallen away, as is so often the case in *Cryptocrinus*, *Glyptosphæra*, and *Stephanocrinus*. The probability of this will be apparent to any one who will compare Angelin's figures of the peristome in the two former genera, the orals being preserved in some individuals and not in others †. Examples of *Stephanocrinus angulatus*, showing corresponding conditions, are represented on pl. xix. of the British Museum 'Catalogue of Blastoidea.' Miller figures and describes these oral plates in *S. Hammelli* and *S. Osgoodensis* ‡; but his nomenclature is, as usual, some years behind the times. For he does not, like other palæontologists, recognize them as oral plates, reserving this name for the interradials or deltoids, a view abandoned long since by the authors

* Seventeenth Report, Geol. Surv. Indiana, pl. ii. figs. 4, 6, pl. iii. figs. 2, 6.

† *Op. cit.* tab. xi. figs. 1, 2, tab. xii. figs. 3–5.

‡ Seventeenth Report, Geol. Surv. Indiana, pp. 23, 25, pl. vi. figs. 3, 7.

of the Blastoid Catalogue and also by Messrs. Wachsmuth and Springer. It is quite refreshing, however, to find him speaking of "the central part of the ambulacral area or mouth." Why cannot he always do so?

Miller likewise gives a good figure showing the summit-plates in his new species *Caryocrinus Indianensis* *. The six central plates, orals, as I regard them, are plainly visible; but the two anterolaterals are separated from the interradials (13, 18) by smaller plates, instead of coming into direct contact with them, as in the specimens of *C. ornatus* kindly lent me by Mr. Wachsmuth, one of which I have figured (Pl. I. fig. 14). I do not remember that the latter condition has yet been described in *Caryocrinus*, though it possibly presents itself in the specimens figured by Hall † and Zittel ‡. It is a point of some importance as regards the homologies of these summit-plates, for in *Stephanocrinus*, *Elæacrinus*, and in some species of *Platycrinus*, the orals also come into direct contact with the interradials. In Mr. Wachsmuth's specimen the tegmen is much depressed along the lines of these two anterolateral interradials, and Miller says that in *C. Indianensis* it is "depressed, convex, and sunken between the arm clusters so as to give it a wavy surface. The central plate is large, heptagonal; it is surrounded by seven plates that cover nearly the whole summit. Two of the seven plates curve upward and surround two-thirds of the prominent azygous opening." The central plate, together with five of the seven around it, are the orals, the other two belonging to the anal system, just as is shown in Hall's figures of the summit of *C. ornatus*, or in Mr. Wachsmuth's specimens. Miller, however, describes the "vault" of *C. Indianensis* as "different from that of *C. ornatus*, the structure of which Wachsmuth thought was generic." But the only point of difference is that in some individuals of *C. ornatus* a third anal plate comes up into line with the other two, just behind the posterior oral; and this led Wachsmuth to describe the latter as surrounded by eight plates §, while Miller only finds seven in *C. Indianensis*. This difference, however, is certainly not of specific value, and I am inclined to think that the same may be said of the other characters on which Miller founded the species *Caryocrinus Indianensis*.

* *Ibid.* p. 19, pl. v. fig. 10.

† 'Palæontology of New York,' vol. ii. pl. 49. fig. 1 *v*, pl. 49 *a*. fig. 1 *e*.

‡ 'Palæontologie,' Bd. i. p. 419, fig. 295 *b*.

§ See *suprà*, pp 19, 20.

EXPLANATION OF PLATE I.

Fig. 1. Analysis of the dorsal cup of *Hemicosmites pyriformis*. Copied from Von Buch (Abhandl. Berlin Akad. 1844, Taf. ii. fig. 10).—*ib*, 1–4, infrabasals; *b*, 5–10, basals; *r*, 11, 12, 14–17, radials; *i*, 13, 18, A, interradials.

Fig. 2. Analysis of the dorsal cup of *Caryocrinus ornatus*. Copied from Hall ('Palæont. New York,' vol. ii. pl. 49. fig. 1 *y*).—Lettering as in Fig. 1.

Figs. 3–7. A–E, the five rays; 1–4, infrabasals; 5–9, basals; 10–14, radials; 15–19, first series of perisomic plates (interradials ?).—N.B. The numbering of the plates is not always identical with that employed in the original figures.

Fig. 3. Analysis of the dorsal cup of *Echinoencrinus armatus*, var. Copied from Forbes (Mem. Geol. Survey, vol. ii. pl. xix. fig. 5) with the addition of a pore-rhomb, occasionally present on plates 12–18.

4. The dorsal cup of *Echinoencrinus angulosus*, developed laterally. Copied from Von Buch (Abhandl. Berlin Akad. 1844, Taf. ii. fig. 7).

5. Analysis of the dorsal cup of *Callocystis Jewetti*. Copied from Hall ('Palæontology of New York,' vol. ii. pl. 50. fig. 11).

6. Analysis of the dorsal cup of *Lepadocrinus Gebhardi*. Copied from Hall ('Palæontology of New York,' vol. iii. pl. 7. fig. 23).

7. Side view of the calyx of *Cystoblastus Leuchtenbergi*. Copied from Volborth (Mém. St. Pétersbourg Acad. 1870, tome xvi. no. 2, fig. 14). —*b*, osculum; *c*, excretory (?) opening,

8. The dorsal cup of *Glyptocystis multipora*, developed laterally. Copied from Quenstedt 'Atlas, Asteriden und Encriniden,' tab. 113. fig. 83.

9. The dorsal cup of *Cryptocrinus cerasus*, developed laterally. Based on Von Buch's figure (Abhandl. Berlin Akad. 1844, Taf. ii. fig. 5).

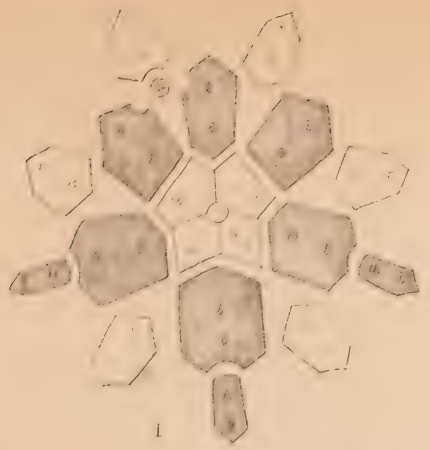
Figs. 10, 11. Internal and external views of the oral pole of *Pyrocystis desiderata*. Fig. 10 shows the subtegminal ambulacra (hydrophores, *Barrande*), and fig. 11 the low pyramid of oral plates above the mouth. Copied from Barrande (Syst. Silur. de Bohême, vol. vii. pl. 29. figs. 32, 33).

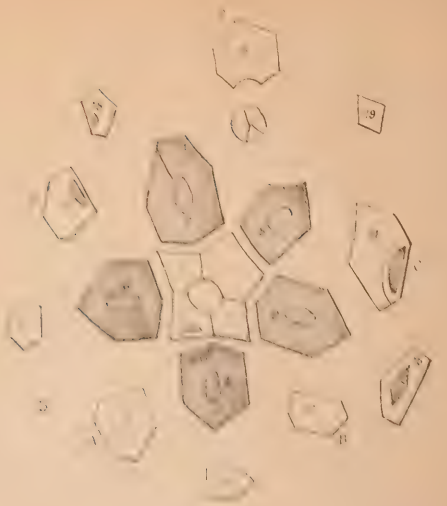
Fig. 12. The oral pole of *Aristocystis Bohemica*. Copied from Barrande (Syst. Silur. de Bohême, vol. vii. pl. 9. fig. 17).—*a*, mouth; *b*, anus; *c*, genital pore; *d*, excretory (?) opening. The genital pore is on the edge of the anal opening.

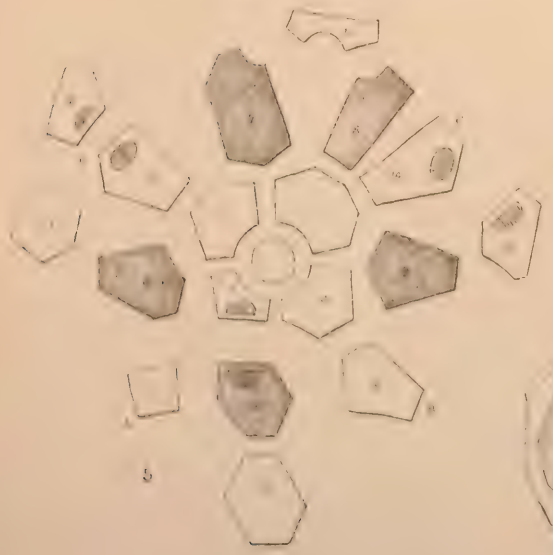
13. A similar view of another specimen, with the genital pore further removed from the anal opening. Copied from Barrande (Syst. Silur. de Bohême, vol. vii. pl. 9. fig. 6).

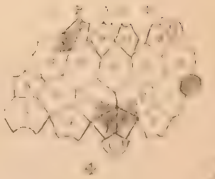
14. Summit of *Caryocrinus ornatus*, from a specimen belonging to Mr. Wachsmuth.—*b*, anus; *o*, oral plates; *r* (11, 12, 14–17), radials; *i* (13, 18), interradials.

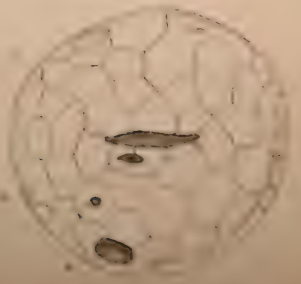
15. Portion of the summit of *Glyptosphæra Leuchtenbergi*, showing—*a*, the low pyramid of oral plates above the mouth; *b*, the anus; *c*, the genital pore; *d*, the excretory (?) opening, possibly a madreporite. From Quenstedt 'Atlas, Asteriden und Encriniden,' tab. 114. fig. 10.

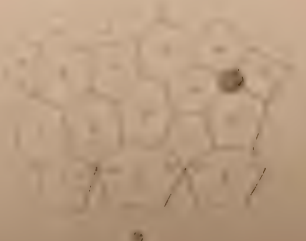


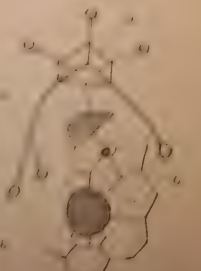












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